A thesis entitled

TRILOBITES OF THE FAMILY CALYMENIDAE FROM THE ORDOVICIAN, SILURIAN AND DEVONIAN SYSTEMS OF NORTH-WEST EUROPE

Submitted for the degree of

DOCTOR OF PHILOSOPHY

in the

FACULTY OF SCIENCE

UNIVERSITY OF LEICESTER

by

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Volume 1, text

December, 1973

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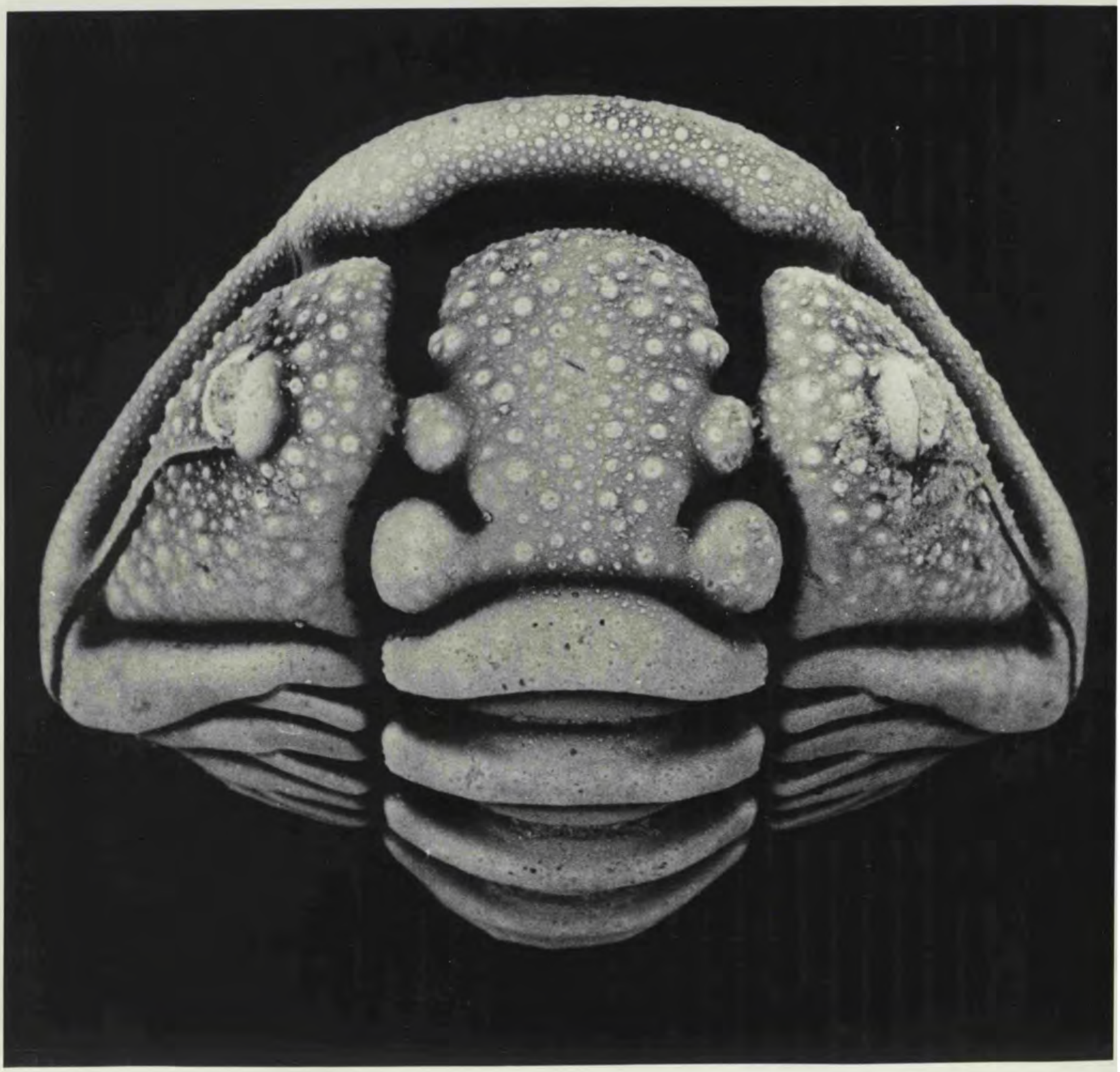

Dedicated to my wife and parents,
for their constant encouragement and the
interest they have shown in my studies.

ABSTRACT

This work represents a revisional study of many of the species of the family Calymenidae Milne Edwards, 1840 (Trilobita) from the Ordovician, Silurian and lower Devonian of NW Europe. Taxa from Britain, Norway, Sweden and Czechoslovakia have received particular attention, and, where appropriate comparisons have been made with non-European species. Most of the chapters are arranged on a taxonomic basis; one deals with the calymenid fauna from a single region (Middle Ordovician calymenids from Norway), and another is concerned with some evolutionary trends in Ordovician and Silurian species (Chapter F). One new subfamily (Flexicalymeninae), three new genera (*Quadricalymene* , *Tapinocalymene*, *Palacalymene*), and thirteen new species are erected.

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ACKNOWLEDGEMENTS.

My sincere thanks are due especially to Professor P.C. Sylvester-Bradley for allowing me to undertake this study in his department, for the interest he has shown in the project, and for the supervision he has given me during the last three years. I am also grateful to Dr. J.H. McD. Whitaker for his supervision in the initial stages of this Ph.D, and his help throughout with problems regarding Silurian stratigraphy. Professor H.B. Whittington (University of Cambridge) has generously given of his time to discuss various aspects of the work.

I am indepted to the following persons who have kindly allowed me to loan material in their care: Dr. R.A. Fortey and Mr. S.F. Morris, British Museum (Natural History); Dr. I. Strachan, University of Birmingham; Dr. H.C. Nisbet, Grant Institute of Geology, University of Edinburgh; Dr. A.W.A. Rushton, Institute of Geological Sciences, London; Dr. J.K. Ingham and Dr. W.D.I. Rolfe, Hunterian Museum, University of Glasgow; Dr. I. Chlupac and Mr. Galle, Ustredni Ustav Geologicky, Prague; Dr. J. Bergström, Palaeontologiska Institutionen, University of Lund; Mr. W.J. Norton, Ludlow Museum; Dr. L. Marek, Ceskoslovenska Akademie ved Geologicky Ustav, Prague; Dr. H. Jaeger, Palaontologisches Museum, Humboldt Universitat, Berlin, DDR; Mr. M. Jones, Leicester City Museum; Dr. M.G. Bassett and Dr. R.M. Owens, National Museum of Wales, Cardiff; Dr. D.L. Bruton, Palaeontologisk Museum, Oslo; Dr. V. Jaanusson, Naturhistoriska Riksmuseet, Stockholm; Dr. C.D. Waterston, Royal Scottish Museum, Edinburgh; Dr. R. Skögland, Sveriges Geologiska Undersökning, Stockholm; Dr. R.B. Rickards and Dr. C.L. Forbes, Sedgwick Museum, Cambridge; Dr. W. Struve, Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt am Main; Mr. B.R.P. Playle, Wollaton Hall Natural History Museum, Nottingham;

Professor R.A. Reyment and Professor P. Thorslund, Paleontologiska Institutionen, Uppsala; Dr. J.E. Merida, Smithsonian Institution, Washington.

Specimens were also made available to me through the kindness of Dr. J. Shirley; Mr. David J. Siveter, University of Leicester; Dr. P. D. Lane, University of Keele; Dr. J.Dalingwater, University of Manchester; Dr. J. Miller and Mr. J. Tipper, University of Edinburgh; Dr. J.F. Cutler, Idaho State University; Mr. D. Mikulic; Mr. R. Marsh, Norwood Technical College, London; Dr. J.H. McD. Whitaker, University of Leicester.

During the course of this study, three months were spent in Norway, Sweden and Czechoslovakia. For about seven weeks of this time I examined material at the Palaeontologisk Museum, Oslo, and I greatly appreciate the help and hospitality given me, and the facilities put at my disposal, by Professor G. Henningsmoen and Dr. D.L. Bruton. I wish also to thank Dr. Bruton and Mr. F. Bockelie for their guidance in the field, and the latter for his assistance when I was in Stockholm. My stay in Czechoslovakia was made particularly enjoyable and rewarding through the efforts of Dr. L. Marek, to whom I am deeply grateful for his companionship while in Prague, and for showing me field localities. I also extend my gratitude to Dr. R. Horny who allowed me to make casts of Barrande's specimens, and to examine the calymenid collections of the National Museum.

Throughout the period of study the author has been self-financed, though some monetary aid has been provided by the Jane Handley Foundation Trust, Wednesbury, Staffordshire, and some was received from the Research Board of Leicester University towards the cost of the foreign excursion. I gratefully acknowledge the receipt of both these grants.

I am appreciative of the assistance given me by all the technical staff of the Leicester Geology department and the personnel of the central photographic unit. Mr. R. Branson and Mrs. J. Westerman have given advice and help in the preparation of some of the drawings, Mr. G. McTurk gave me an introduction to macrophotography and has taken stereoscan photographs, and Mrs. A. Boustead has kindly translated French and German texts. I am also most grateful to Miss S. Ward for typing part of the text and for help in the preparation of the bound volume.

Finally I wish to sincerely thank my wife for the incalculable assistance and support she has given me, and to my parents for the sacrifices they have made in furthering my education.

ABBREVIATIONS.

The following is a list of abbreviations used to denote the repository of the specimens referred to in the text. The material studied is derived from four main sources: National and provincial museums, National Geological Surveys, Universities, and private collections.

BM	British Museum (Natural History).
BU	University of Birmingham.
DJS	Derek J. Siveter.
GIG	Grant Institute of Geology, Edinburgh.
GSC	Geological Survey of Canada.
GSM	Institute of Geological Sciences.
HM	Hunterian Museum, Glasgow.
I Ch	Dr. I. Chlupac, Ustredni Ustav Geologicky, Prague.
IG	Museum of the Geological Institute, Warsaw.
IPLU	Paleontologiska Institutionen, University of Lund.
IPU	Paleontologiska Institutionen, Uppsala.
J Ti	Mr. J. Tipper, University of Edinburgh.
LE	Leintwardine Collections of Dr. J.H. McD. Whitaker, University of Leicester.
LM	Ludlow Museum.
L Mk	Dr. L. Marek, Ceskoslovenska Akademie ved Geologicky Ustav, Prague.
M	Mr. R. Marsh, Norwood Technical College, London.
MB	Palaontologisches Museum, Humboldt Universitat, Berlin, DDR.
MCZ	Museum of Comparative Zoology, University of Harvard.
MJ	Mr. M. Jones, Leicester City Museum.
NMI	National Museum of Ireland, Dublin.

NMP Narodni Museum, Prague.

NMW National Museum of Wales, Cardiff.

P La Dr. P. Lane, University of Keele.

PMO Paleontologisk Museum, Oslo.

RM Naturhistoriska Riksmuseet, Stockholm.

RO Dr. R.M. Owens, National Museum of Wales, Cardiff.

RSM Royal Scottish Museum, Edinburgh.

SGU Sveriges Geologiska Undersökning, Stockholm.

SM Sedgwick Museum, Cambridge.

SMF Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt am Main.

WM Wollaton Hall Natural History Museum, Nottingham.

USNM Smithsonian Institution, Washington.

UUG Ustredni Ustav Geologicky, Prague.

TERMINOLOGY.

The terminology is the same as that employed in the 'Treatise of Invertebrate Palaeontology' (Moore, 1959, pp. O117-O126), but with the following exceptions. The glabella has been taken to include the occipital ring, and fixed and free cheek have been used instead of fixigena and librigena. A few terms not present in the treatise have been adopted:

Eye socle - coined by Shaw & Ormiston (1964, p. 1002) for the platform on the upper part of the free cheek which lies below the visual surface of the eye.

Border and doublure sectors - introduced by Campbell (1967, p. 25) for the outer and inner parts respectively of the calymenid rostral plate.

Cincture - used by Campbell (1967, p. 26) to describe the peripheral impression on the pleural region of the pygidium which reflects the position taken by the lateral border of the cephalon during enrollment.

Intermediate lobe - employed by Shirley (1931, 1933, 1936) to describe the small lobe often found in calymenids on the side of the median glabellar lobe, at the adaxial end of lateral glabellar furrow 1p. (= supplementary lobe of Whittington 1971, pp. 460, 462).

TECHNIQUES.

SPECIMEN PREPARATION. The majority of specimens have been prepared with the use of a Burgess Vibro Tool, together with needles and brushes. An air-abrasive machine was also employed and found to be particularly helpful in cleaning the hypostomes of specimens which were inaccessible under other mechanical preparation methods. Sodium bicarbonate was the powder used for removing the matrix on or near the hypostome, the bulk of the sediment having been previously stripped off with the Vibro Tool.

CASTING. 'Silcoset' silicone rubber has been used throughout for taking casts of external mould specimens. The silicone rubber was darkened by adding carbon black to the gel before tipping it in the external mould to solidify.

In instances where it has not been possible to loan museum material (eg. Barrande Collection, National Museum, Prague), replicas were made of the required specimens for subsequent examination in Leicester. The process involved was to take a silicone rubber negative of the specimen, and then to make a positive cast using a dental paste.

PHOTOGRAPHY.

a) Photographing. All macrophotography has been undertaken by the present author at Leicester, using Leitz aristophot equipment.

i) Camera. Leica MD 35 mm.

ii) Lenses. 12 cm Summar for most work. 6.5 cm Milar for small specimens and detailed shots of ornamentation.

iii) Film. Addox KB14 was used initially, but the majority of specimens have been taken on Kodak Panatomic - X.

iv) Lighting. A fluorescent ring light was used for general lighting; this was supplemented by a single source of light from the top left hand (NW) side of the specimen.

v) Stereo-photography. Very few modern workers on trilobites illustrate their material by the use of stereo-pair photographs, and as far as I am aware only Evitt and Whittington (1953), Ross (1967) and Chatterton (1971) have figured calymenids in this fashion. The advantages of a three dimensional representation of the fossil are obvious, and Evitt (1949) and others have long advocated the widespread application of this technique. The stereo-pair approach in palaeontology is used extensively in the Leicester department, and I have applied it throughout this work, though due to the various restrictions imposed by journal size and the number of plates made available, it has not been possible to finally figure all specimens in this way.

In order to obtain a stereo-pair each specimen was tilted on a rotational stage through an angle of about five degrees. Where possible and for optimum viewing, most stereo-pairs have been mounted on the plates at a distance of 55 mm apart.

vi) Coating. Prior to a light coating of ammonium chloride sublimate, many of the specimens were first covered with a thin film of dilute opaque.

b) Developing. Patersons Acutol was used at all times.

c) Printing. Grades 2 and 3 of Kodak photographic paper have been used extensively; very rarely grades 1 and 4. The enlarger employed was a Leitz focomat Ic.

MEASUREMENTS.

METHOD OF MEASUREMENT. An ocular micrometer in a binocular microscope has been used for taking most measurements. Calipers were used for large measurements.

ORIENTATION OF SPECIMENS. Cranidia were oriented with the posterior margin of the occipital ring vertical; pygidia with the plane of the ventral margin of the border roll horizontal.

MEASUREMENTS TAKEN. Many of the measurements taken and the symbols used to denote these measurements are the same as those employed by Hughes (1969).

1) Cephalon.

A	Sagittal length of cephalon.
B	Sagittal length of glabella.
B_1	Sagittal length of glabella minus occipital ring.
B_2	Sagittal length of frontal glabellar lobe.
B_3	Exsagittal length of palpebral lobe.
B_4	Exsagittal length of 1p lateral glabellar lobe.
C	Postocular length measured between the posterior margin of the palpebral lobe and the posterior margin of the glabella, as projected onto the sagittal line.
C_1	Length of fixed cheek between a line projected transversely from the occipital furrow and the junction of the anterior branch of the facial suture and the lateral border furrow.
D	Sagittal length of preglabellar area.
D_1	Sagittal length of preglabellar furrow (*Gravicalymene*, *Diacalymene* and *Tapinocalymene*) or preglabellar field (*Pharostoma*).
I	Transverse width of cranidium.
J	Transverse width of cranidium between junction of anterior branch of facial suture and anterior margin.
J_1	Transverse width of cranidium between posterior margins of palpebral lobes.
J_2	Transverse width of cranidium between anterior margins of palpebral lobes.
K	Transverse width of glabella at occipital ring.
K_1	Transverse width of glabella at 1p lobes.

K_2 Transverse width of glabella at 2p lobes.

K_3 Transverse width of glabella at 3p lobes.

K_4 Transverse width of glabella at 4p lobes.

K_5 Transverse width of frontal glabellar lobe.

2) Pygidium

W Transverse width of pygidium.

X Transverse width of axis at anterior margin.

X_1 Transverse width of axis at posterior (last) ring furrow.

Y Sagittal length of axis.

Y1 Sagittal length of terminal axial piece.

Z Sagittal length of pygidium.

3) Hypostome.

a Sagittal length of hypostome.

b Exsagittal length between a line projected transversely from the anterior margin at the median line and the posterior margin of the posterior spine.

b_1 Exsagittal length between a line projected transversely from the anterior margin at the median line and the posterior wing.

b_2 Sagittal length between anterior margin and median furrow.

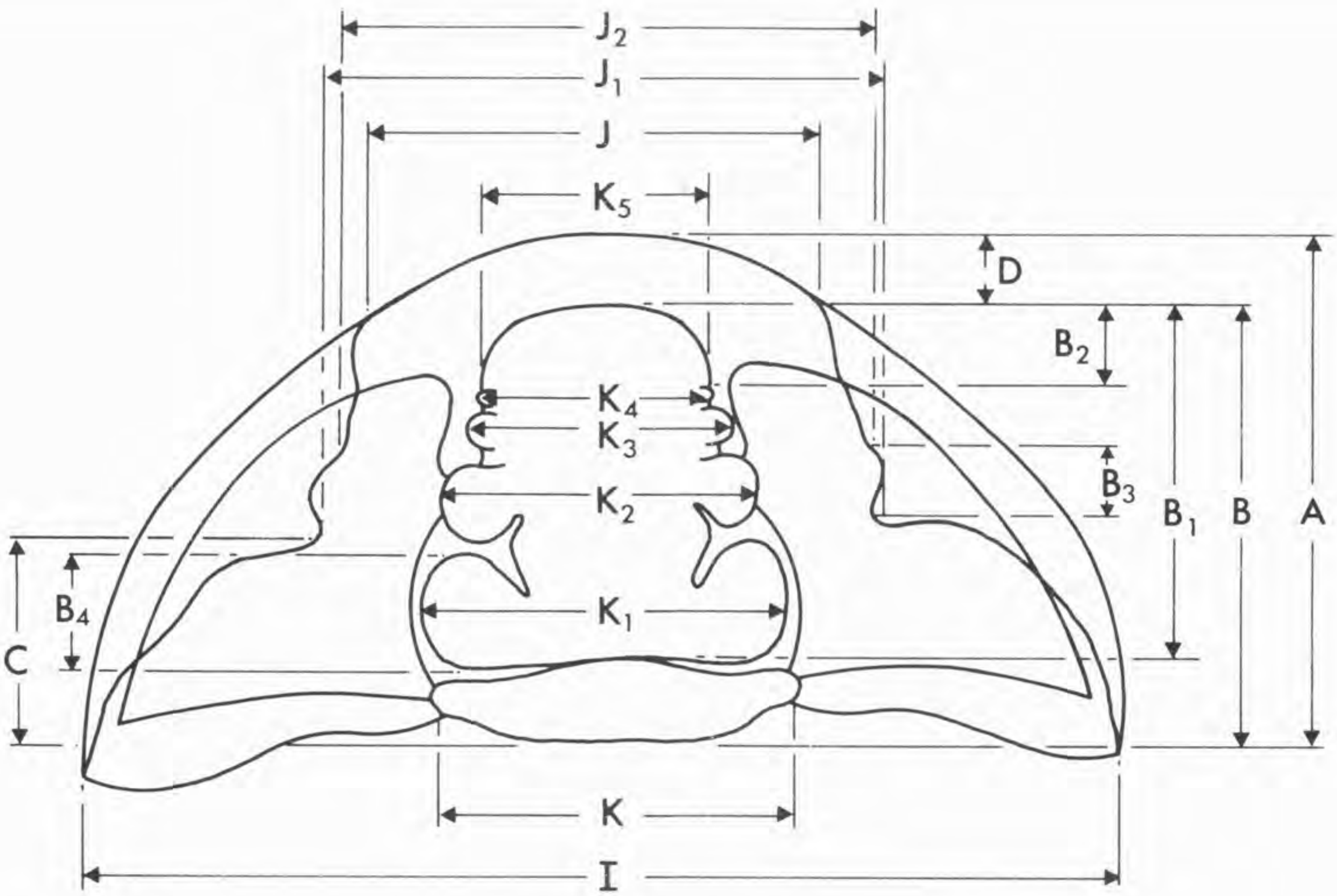
b_3 Sagittal length between anterior margin and most inflated part of the anterior lobe.

d Transverse width at anterior wings.

e Transverse width at posterior wings.

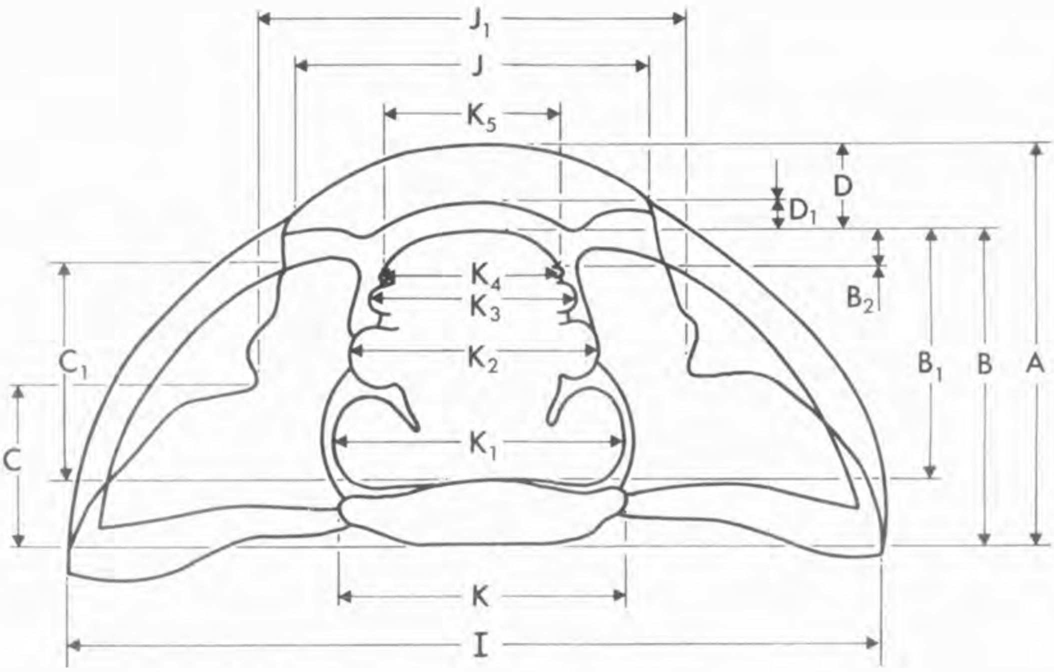
e_1 Transverse width at posterior spines.

e_2 Transverse width between adaxial, dorsal margins of posterior spines.



MEASUREMENTS TAKEN ON CEPHALON OF *Calymene*

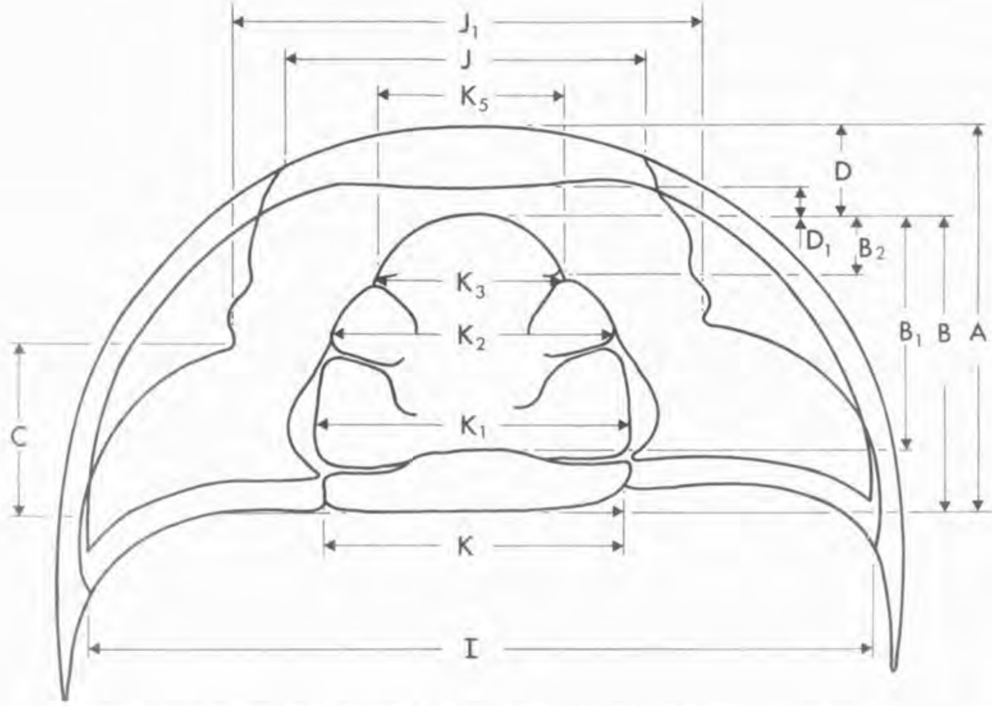
TEXT- fig 1



MEASUREMENTS TAKEN ON CEPHALON OF

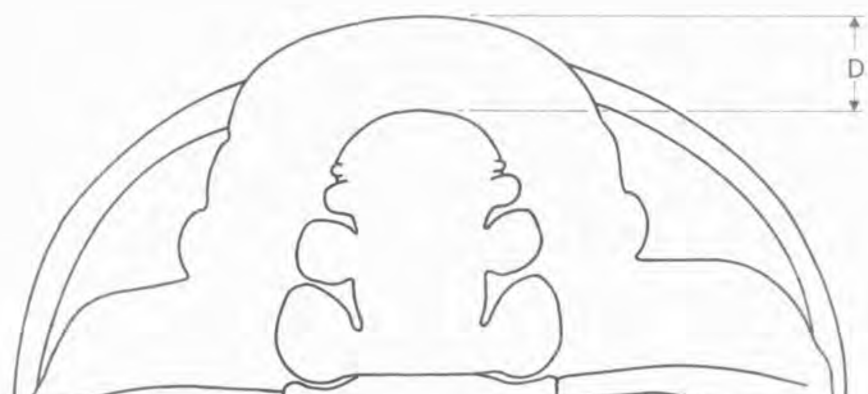
Diacalymene and *Gravicalymene*

TEXT-fig. 2



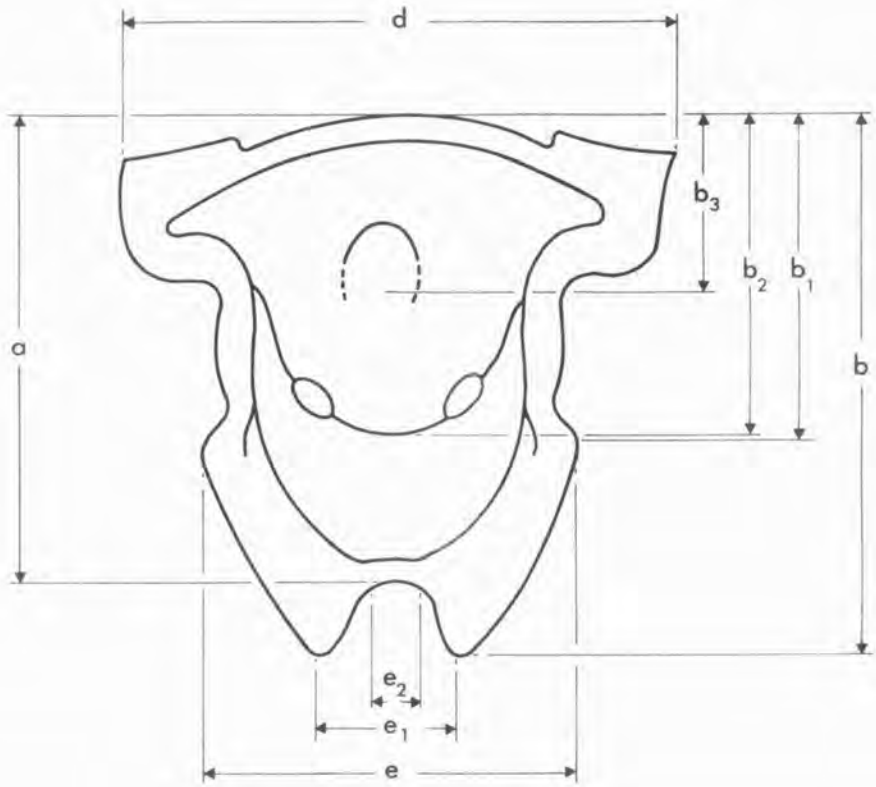
MEASUREMENTS TAKEN ON CEPHALON OF *Pharostoma*

TEXT- fig. 3



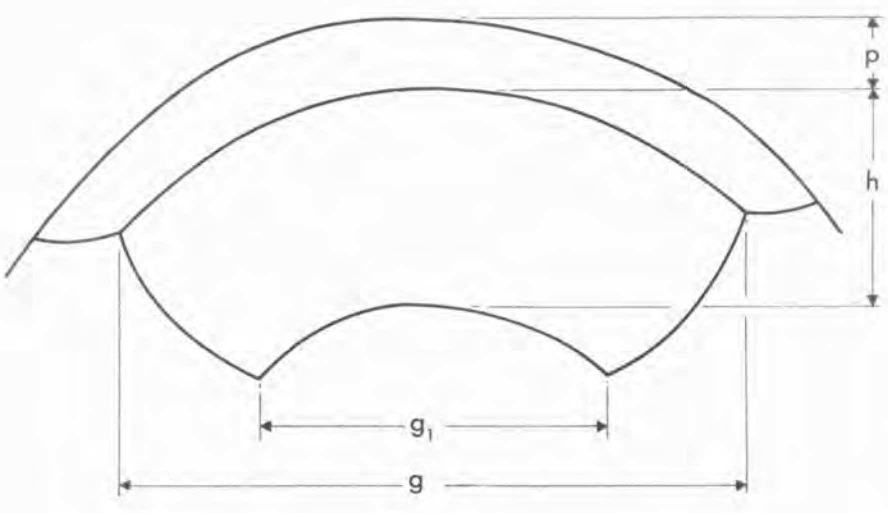
Flexicalymene

TEXT - fig. 4



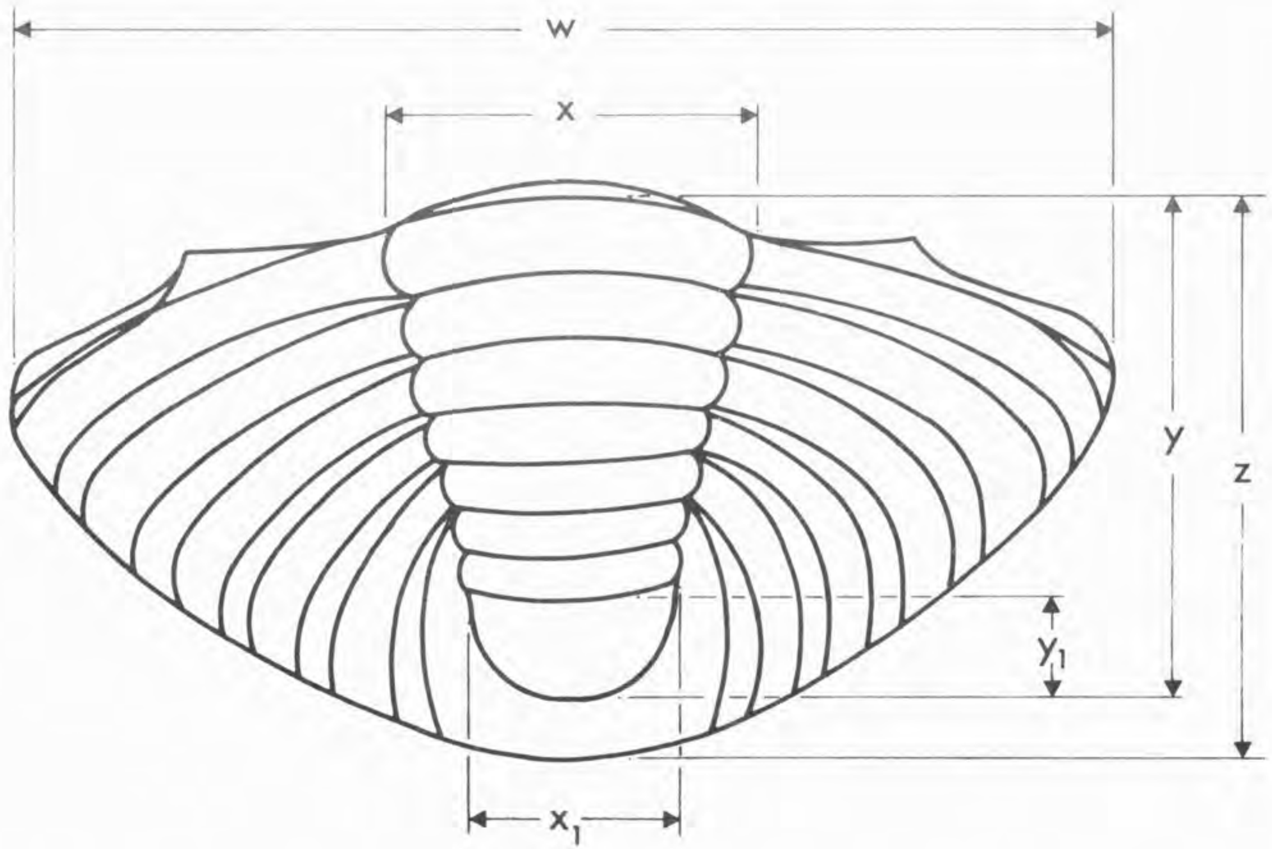
MEASUREMENTS TAKEN ON CALYMENID HYPOSTOME

TEXT - fig. 5



MEASUREMENTS TAKEN ON CALYMENID ROSTRAL PLATE

TEXT - fig. 6



MEASUREMENTS TAKEN ON CALYMENID PYGIDIUM

TEXT - fig. 7

4) Rostral plate.

g Transverse width at rostral suture.

g_1 Transverse width at inner arc of border sector.

h Sagittal length.

5) Anterior border of cranidium.

p Sagittal length of outer face of anterior border of cranidium.

SCATTER DIAGRAMS. In the scatter diagrams (Chapter E) the symbols used to denote the specimens of the various species have sometimes been enclosed with, or represented by, a circle. Where this is the case the measurements for one or both of the variates has been estimated. A list of measurements is given in Vol. 2, Appendix 1.

HISTORY OF RESEARCH.

The family Calymenidae are an important and ubiquitous group of lower Palaeozoic trilobites. They range from the Tremadoc into the Devonian and have world-wide occurrence. They are ill-represented in Tremadoc rocks but often constitute a significant part of many Ordovician and Silurian fauna's.

The type genus, Calymene, was established by Brongniart (1822), and the family was founded by Milne Edwards (1840). In the last century the following authors added much to our knowledge of the group, and some of them attempted to rationalize the classification thereof: Beyrich (1846), Berrande (1846, 1852, 1872), Salter (1865), Schmidt (1894, 1907), Pompeckj (1898).

In the early part of the present century somewhat less attention was given to the group. Our understanding of the major groupings within the Calymenidae owes much to the studies of Shirley (1931, 1933, 1936). More recently the papers of Whittington (in Moore 1959, 1971), Dean (1962, 1963, 1965, 1971), Whittard (1960), Ross (1967), Schrank (1970), and Campbell (1971) have made considerable contributions to our taxonomic appreciation of the family. There are many other works, too numerous to list here, in which calymenids figure as part of a faunal treatment.

This thesis has attempted to survey at first hand as much British and European material as possible.

It has proved impractical to finally treat here all of the material the author has examined. It is intended to publish all of the findings of this study in due course.

THE CALYMENID GENUS PHAROSTOMA FROM THE ORDOVICIAN OF BRITAIN, SCANDINAVIA AND BOHEMIA.

INTRODUCTION. In his monograph of the Ordovician trilobites of West Shropshire, Whittard reviewed all known members of Pharostoma though only dealt with specimens from the Hope Shales (Llanvirn) at first hand. The present work has included a study of Scandinavian, Czechoslovakian, and British forms.

Although Pharostoma is geographically widespread, specimens of the genus are not found in abundance and one is often hindered by a lack of material. No species has previously been based on British material though Whittard (1960, p. 132), Whittington (1965, p. 55) and Dean (1971, p. 42) have described Shelve Inlier, Bala, and Chair of Kildaire Limestone material respectively, and Ingham (1966, p. 487) has made reference to a northern England representative. Some species have been erected on the basis of a single cranidium or poorly preserved collections and the need is still felt for a revision of the more geographically remote taxa, many of which are not readily accessible for examination (P. parapulchrum Kobayashi, 1951 from the lower Ordovician of China; P. denticulatum (Eichwald, 1860) from the lower Ordovician of the U.S.S.R.). Other species from the Baltic and the N European Plain (P. pedilobum Roemer, 1861) have been founded on specimens from erratic boulders, and this has created special problems regarding their original geographical and stratigraphical provenance.

Despite these shortcomings, it has been possible to delimit several species groups from the Ordovician of NW Europe.

THE SUPRAGENERIC POSITION OF PHAROSTOMA AND ITS RELATIONSHIP TO OTHER EARLY ORDOVICIAN CALYMENIDS.

The detailed treatment of this problem lies outside the scope of the present study, though it is intended to deal fully with this subject at a later date. However a few comments are appropriate here. Preliminary studies accord with the proposition (Dean 1965, p. 8) that the family Pharostomatidae Hupe, 1953 is a junior synonym of Bathycheilinae Pribyl, 1953. Contrary to the opinion of Dean (1965, 1966, p.297), I believe that both Bathycheilus and Pharostoma are true calymenids (s.s.), and that any suprageneric grouping including these taxa should not be excluded from the Calymenidae. Other early genera which show primitive features characteristic of Pharostoma and Bathycheilus include Pharostomina Sdzuy, 1955 and Protocalymene Ross, 1967. The morphological similarities exhibited by all these genera (which are generically distinguished below) may provide a basis for their inclusion within a single subfamily. Apart from the long-ranging Pharostoma (Arenig to Ashgill), the remaining genera are confined to a relatively short part of the stratigraphical column (Tremadoc - Llanvirn).

Family CALYMENIDAE Milne Edwards, 1840

Subfamily Bathycheilinae Pribyl, 1953

Genus PHAROSTOMA Hawle & Corda, 1847

(= Prionocheilus Rouault, 1847; nomen oblitum)

TYPE SPECIES. Calymene pulchra Beyrich, 1846, pl. 2, figs. 6a, b; from the Ordovician Letna Formation (lower Caradoc), Vesela near Beroun, Czechoslovakia. By monotypy.

OTHER SPECIES. P. costai Thadeu, 1947; P. denticulatum (Eichwald, 1860); P. foveolatum (Törnquist, 1884); P. leptaenarum (Tornquist, 1884); P. liluensis Reed, 1915; P. matutinum (Dean, 1966); P. narinosum sp. nov.; P. nieszkowskii Schmidt, 1894; P. obtusum (McCoy, 1846); P. oelandicum Angelin, 1854; P. ornithoreos sp. nov.; P. pulchrum (Beyrich, 1846); P. parapulchrum Kobayashi, 1951; P. pedilobum (Roemer, 1861); P. rarum Cooper & Kindle, 1936; P. simile Thorslund, 1940; P. verneuili (Rouault, 1847); P. vokovicense Snajdr, 1956; P. ? mendoza Rusconi, 1953.

DIAGNOSIS. Glabella is subrectangular to parabolic in outline. Three pairs of lateral glabellar furrows, 1p often abaxially shallow, 3p very short (tr.) and faint. Lateral glabellar lobe 3p very weakly inflated. Side of central glabellar lobe usually gently to moderately convex at inner end of 1p furrow. Axial furrow flat-bottomed, crescent-shaped and distinctly widest beside lobe 1p. Preglabellar field varies from about one-tenth to more than half as long as glabella. Eye ridge may be present. Free cheek bears relatively long genal spine (which is partly composite with fixed cheek), and row of close-set lateral marginal spines from junction of border and doublure which are continued onto rostral plate. Hypostome has fringing subsidiary spines on abaxial margin of main posterior spine. Thorax with thirteen segments. Pygidium has maximum of thirteen axial rings, eleven pleural furrows.

DISCUSSION.

Nomenclature: Pharostoma or Prionocheilus ?

The history of this taxon is an unhappy one. Opinion is divided over the use of Pharostoma or Prionocheilus as the valid generic name; if one accepts Pharostoma then the authorship of the type species, Pharostoma pulchrum, is in dispute.

In 1964 Dean demonstrated that Prionocheilus Rouault, 1847 antedates Pharostoma Hawle & Corda by some three months. He advocated retaining the senior synonym in preference to the more widely used junior name largely because the type species, Prionocheilus verneuili Rouault, 1847 had been redescribed and reillustrated by Bezier (1907). Whittington (1965, p. 56) rejected Dean's proposal because Prionocheilus had "not been used by workers on calymenids"; he thus made use of Article 23(b) of the International Code of Zoological Nomenclature, 1961, and considered Prionocheilus a nomen oblitum. Dean (1971, p. 42) later reaffirmed his views, supporting his case on the basis that "with the exception of Shirley (1936), no comprehensive revision of the calymenid trilobites has been undertaken, and all works dealing with Pharostoma have included it only as part of larger, more varied faunas (for example Snajdr 1956; Whittard 1960). Furthermore, Shirley dealt only with British calymenids and apparently excluded Pharostoma because he considered it only doubtfully a calymenid ...... Consequently it is felt that the normal conditions for a nomen oblitum are not satisfied ......".

Nevertheless Prionocheilus has remained unmentioned as a senior synonym in primary zoological literature for more than fifty years preceding its discovery as such and, as the law stands, must be considered a 'forgotten name'. Although Article 23(b) is so worded as to concentrate on the suppression of unused older names, its fundamental aim is the protection of the unchallenged junior synonym and to preserve stability of nomenclature. There can be no doubt of Pharostoma being universally used in zoological publications from 1914-1964. It was employed by at least twenty palaeontologists in as many papers during this time and although the genus was not individually revised, these facts stand strongly against any proposition which asserts neglect of the taxon. Pharostoma is therefore entrenched in the literature and it is threatened by the laws of priority; Article 23(b) comes automatically into effect and can only be laid aside by express direction of the Commission - to which Dean must apply before his view can be adopted.

A discussion of the authorship of the type species will be found under Pharostoma pulchrum pulchrum.

Differences of Pharostoma from other genera.

Pharostoma is most closely related to Pharostomina Sdzuy, 1955. The great similarity of P. öpiki, the type species of Pharostomina, to Pharostoma matutinum (Dean, 1966) from the Arenig of the Montagne Noire supports this proposed relationship (cf. Dean 1966, p. 304, pl. 10, figs. 1-7 with Sdzuy 1955, pl. 6, figs. 62-88), as does their geographical and stratigraphical proximity. Pharostomina differs in that it lacks cephalic lateral marginal spines, has shorter genal spines, a less conspicuous crescentic area of the axial furrow outside the basal glabellar lobe and complete absence of any inflation (= "oval area" of Whittington in Moore 1959) on the side of the central glabellar area at the adaxial end of lateral furrow 1p.

Differences of Bathycheilus Holub, 1908 from Pharostoma include a much less parabolic (subtrapezoidal to bell-shaped) glabellar outline, absence of "oval-areas", no posterior constriction to the crescentic area beside lateral lobe 1p, a much larger librigenal spine, and apparently a lack of any cephalic marginal spines (after Dean, 1965, p. 8). Other distinctions appear to be the much deeper cranidial axial furrow, a more swollen, convex glabella and fixed cheek, and a less discrete preglabellar field.

Protocalymene Ross, 1967 is similar to Bathycheilus in differing from Pharostoma in the shape and convexity of its glabella, its deeper axial furrow, more inflated fixed cheek and the absence of cephalic marginal spines. In addition, Protocalymene does not seem to have genal spines on the fixed cheek, has a less well developed 2p lobe and 2p furrow, and complete lack of 3p lobe and 3p furrow.

Comparison of British, Bohemian and Scandinavian faunas.

This comparison has brought to light three species groups which are more or less confined by broad geographical and stratigraphical parameters. In discriminating these groups the following characters have proved useful: Glabellar outline, especially that of the frontal lobe; depth and nature of preglabellar furrow; length and form of preglabellar field; type of anterior border; presence or absence of subcircular and oval swellings on the posterior abaxial margin of the preglabellar field and inner part of the fixed cheek respectively.

All of the characters given for each group are not present in every species included, but as a general guide they hold good. It is considered, however, that the distinction between the groups is not sufficient to merit the erection of subgenera.

Group 1.

Includes P. vokovicense Snajdr, 1956; P. pulchrum pulchrum (Beyrich, 1846); P. pulchrum subsp. nov. A

In this group the cranidium may attain a relatively large size; the preglabellar field is quite short (about one seventh or one eighth as long as the glabella); the glabella is in the shape of a broadly based parabola, the outline of the frontal glabellar lobe varies from being bluntly rounded (P. vokovicense) to being more strongly arched though in all cases it is evenly convex; the preglabellar furrow is of about constant depth; there are no marked, individual swellings on the preglabellar field or adaxially from the palpebral lobe on the fixed cheek; the anterior border is roll-like in cross-section, and variably inflated.

The group occurs in strata of Llanvirn, Llandeilo and Caradoc age and is present in Bohemia and Britain. It is also found elsewhere in the Tethyan region, such as the Llanvirn of Portugal and the upper Caradoc of Morocco.

Group 2.

Includes P. denticulatum (Eichwald, 1860); Pharostoma aff. P. denticulatum (of this report); P. nieszkowskii Schmidt, 1894; P. simile Thorslund, 1940; P. foveolatum (Törnquist, 1884); P. narinosum sp. nov.

Cranidia of the stratigraphically later species in this group are known to attain large sizes. P. foveolatum represents the largest recorded member of the genus, specimen IPU Ar469 having a cranidial length of almost four centimetres. The preglabellar field varies from about one sixth to more than half as long as the glabella; the frontal lobe is generally arched forwards medially but is sometimes slightly flattened (tr.) at its apex and is often flattened or indented either side the median line where preglabellar furrow is somewhat deeper; the preglabellar field at the anterolateral margin of the glabella tends to be inflated - in some species a separate, independantly convex swelling is present; a further inflation may be present on the fixed cheek, situated just behind and a little inwards from the palpebral lobe; the dorsal surface of the anterior border is gently convex (sag.), projects moderately to steeply, forwards and upwards from the border furrow.

This assemblage of species ranges from about the lower Llanvirn to the base of the Ashgill and occurs in Norway, Sweden, Estonia and the East Baltic.

Group 3.

Includes P. oelandicum Angelin, 1854; P. pedilobum (Roemer, 1861); P. obtusum (McCoy, 1846); P. ornithoreos sp. nov.; P. leptaenarum (Törnquist, 1884); Pharostoma sp. A (of this report); Pharostoma sp. B (of this report).

This group has the following characters: The cranidia are generally small, rarely reaching the size of the largest cranidia in Groups 1 and 2; the preglabellar field is not long, varies from about one tenth to one fifth as long as the glabella; the glabella appears subrectangular due to the axial furrows being only weakly convergent anteriorly and the bluntly rounded outline of the frontal glabellar lobe; the preglabellar furrow is of uniform depth; there are no discrete swellings on the preglabellar field or fixed cheek; the anterior border is horizontally inclined, or projects moderately forwards and upwards.

Group 3 occurs mainly in Ashgill strata, though it is also found in the topmost Caradoc. It is present in Scandinavia and Britain, and extends to Quebec (P. rarum Cooper & Kindle, 1936; see Dean 1971, p. 44).

The first two groups (Bohemian and Baltoscandian) are of approximately the same age yet geographically separate. They appear to represent two independant lines of evolution, each of which evolved at a different rate. The Bohemian species do not undergo much morphological change from the Llanvirn to the end of the Caradoc except for an increase in the convexity of the anterior border. On the other hand the Scandinavian and Baltic group show a distinct trend towards the loss of a medially pointed anterior margin and a marked elongation of the preglabellar area (from P. denticulatum through P. nieszkowskii to P. foveolatum).

Pharostoma oelandicum is somewhat atypical of group 3 in the outline of its frontal lobe and in terms of morphology and stratigraphy represents a link with group 2 (see discussion of the species below). The Ashgill species in group 3 appear to have descended from middle Ordovician Scandinavian stock, rather than from Bohemian ancestors.

OCCURRENCE. Pharostoma first appears in the Arenig of S France (P. matutinum (Dean, 1966)) and continues throughout the Ordovician, the last representative being P. obtusum (McCoy, 1846) from the Ashgill (Rawtheyan) of Ireland. The genus becomes widely distributed during this time occurring in Quebec, England, Wales, Ireland, Scandinavia, Estonia, France, Bohemia, the Iberian peninsular, Morocco, China, Burma, and perhaps Argentina.

It is first present in Britain during the Llanvirn, though I am not aware of any specimen from either the Llandeilo or Caradoc Series. It reappears in the Pusgillian (Birdshill Limestone) of South Wales and the Cautleyan and Rawtheyan of northern England and N Wales respectively.

The Lower Chasmops Shale (4bα) provides the first specimens of Pharostoma in Norway and it is here confined to strata of approximately Caradoc age, the last species occurring in the Upper Chasmops Limestone (4bδ).

Unexpectedly early is its occurrence in the Raniceps Limestone (=Llanvirn) of Sweden. The genus occurrs intermittently throughout the middle Ordovician, of this country and is finally seen in the Ashgill Boda Limestone.

In Bohemia it ranges from the Sarka to Bohdalec Formations (Llanvirn to Pusgillian).

Pharostoma vokovicense Snajdr, 1956

Plate 1, figs. 1-7.

? 1918 Calymmene (Pharostoma) pulchra Barr; Novak in Novak & Perner, pp. 12, 37, pl. 4, figs. 17-19.

1956 Pharostoma pulchrum vokovicense nov. subsp.; Snajdr, p. 505, pl. 5, fig. 1, pl. 6, fig. 1.

1960 P. pulchrum vokovicense; Whittard, p. 137.

1965 Pharostoma pulchrum vokovicense Snajdr, 1956; Vanek, p. 30, pl. 3, figs. 1, 2, pl. 4, fig. 6.

1966 Pharostoma pulchrum vokovicense; Dean, p. 303.

1966 Pharostoma pulchrum vokovicense SN.; Havlicek & Vanek, p. 51, pl. 5, fig. 11.

1966 Pr. pulcher vokovicensis (SNAJDR, 1956); Destombes, p. 41.

1967 P. pulcher vokovicensis; Dean, p. 313.

HOLOTYPE. An almost complete cephalon and its counterpart; NMP 184/67; figured Snajdr 1956, pl. 5, fig. 1 (internal mould), and here Pl. 1, figs. 1, 3, 5-7.

TYPE STRATUM AND TYPE LOCALITY. Sarka Formation (Llanvirn), brickyard under the Cerveny vrch hill, Vokovice, Prague.

DIAGNOSIS. Preglabellar area and preglabellar field about three tenths and one eighth as long as glabella respectively. Anterior border furrow shallow and broad (sag.). Anterior border low, gently convex in lateral profile, not sharply narrowing (exs.) abaxially. Frontal glabellar lobe is bluntly outlined.

DISCUSSION. P. vokovicense is the earliest member of the genus from Bohemia. Because it is sufficiently distinct I have regarded it as a separate species and not, as originally considered by Snajdr, a subspecies of P. pulchrum. Nevertheless vokovicense is obviously very closely related to P. pulchrum and since the latter is fully described below I have not provided a formal description of the species. Snajdr (1956, p. 530) used the following characters to separate his taxon: A constantly and equally high and wide (sag. & exs.) anterior border; small lateral marginal spines on the free cheek; and the area between the glabella and anterior border (= preglabellar field) being composed of a low, granulated ridge on the posterior half and a flat, smooth area on the anterior half.

Free cheeks of vokovicense showing well preserved marginal spines have not been at my disposal and Snajdr does not figure any. Vanek (1965, pl. 3, fig. 2) illustrated a free cheek with distinctly short spines though it should be noted that on his photograph the rock matrix surrounding these delicate spines has been blacked out. As far as I am aware Snajdr gave equal weight to each of his discriminating characters though Whittard (1960, p. 136) and Dean (1966, p. 303; 1967, p. 313) both emphasized the form of the preglabellar field. There does not seem to me, however, anything particularly unusual in this character. The weak ridge running transversely in front of the glabella is simply a slender adaxial continuation of the inner part of the fixed cheek; this ridge alone represents the preglabellar field, albeit narrow, sandwiched between the preglabellar and anterior border furrows. The smooth area in front of this ridge is just a rather broad, shallow preglabellar furrow which becomes substantially more narrow towards the facial suture. This arrangement is most typical of vokovicense but it may also be present in later Bohemian species and is even closely paralleled in P. oelandicum Angelin, 1854 from the Macrourus Limestone erratics of Öland.

Distinctive of P. vokovicense is the form of its anterior border. In P. pulchrum pulchrum and P. pulchrum subsp. nov. (of this report) this feature is quite strongly swollen medially and much more convex and wide (sag.) here than abaxially; by comparison that of P. vokovicense is not so distended or high and is more uniformly wide from the median line to the facial suture. The rather blunt outline to the frontal glabellar lobe in vokovicense also appears to contribute towards the separation of this species from P. pulchrum. As with other Pharostoma taxa, considerable intraspecific variation exists in the degree of impression of lateral glabellar furrow 3p.

The figured material of Snajdr(1956) and Vanek (1965) does not elucidate the relationship of the posterior section of the facial suture to the genal angle, though I assume Vanek's depiction (1965, p. 31, text-fig. 7) of P. vokovicense, which shows it having a proparian type of facial suture, to be erroneous.

OCCURRENCE. Known only from the Sarka Formation (=Llanvirn) in Bohemia. Apart from the type locality Snajdr also records the species from Osek near Rokycany. Reference by Havlicek & Vanek (1966, p. 26) to P. vokovicense occurring in the Llanvirn of the Shelve Inlier appears to have been dependent upon the known age of the British Strata as Whittards specimens are clearly different. The same two authors (1966, p. 25) also claim that vokovicense occurs in the Griffelschiefer of Thuringia, basing their identification on a reference by R. & E. Richter (1927) to Calymene (Pharostoma) pulchra Barr.. The Richters do not figure any Pharostoma specimens in their paper and Freyberg's (1922, p. 245) earlier recording from the Griffelschiefer of Calymene pulchra was put by them in the synonym of Colpocoryphe inopinata Novak in Perner, 1918.

Pharostoma pulchrum pulchrum (Beyrich, 1846)

Plate 1, figs. 8-11; Plate, 2. figs. 1-6; Plate, 3. figs. 1-8; Plate, 4. figs. 3, 4, 7, 8.

1846 Calymene pulchra; Beyrich, pl. 2, figs. 6a-d.

1846 Calymene Pulchra Barr.; Barrande (pars), p. 27.

1847 Ph. pulchrum; Hawle & Corda, p. 88, pl. 5, ? fig. 49, non fig. 49a.

1852 Calym. pulchra Barr.; Barrande (pars), p. 575, pl. 19, figs. 4, 5, 7-9, ? fig. 1, non figs. 2, 3, 6.

1852 Placoparia Zippei. Boeck; Barrande (pars), p. 106, pl. 29, figs. 37, 38.

1872 Calym. pulchra Barr.; Barrande, p. 36, pl. 16, fig. 27.

1872 Placoparia grandis Corda.; Barrande (pars), p. 104, pl. 8, fig. 49.

non 1906 Calymene pulchra BEYR.; Olin, p. 58, pl. 2, fig. 15.

? 1908 Calymene pulchra Barr.; Delgado, p. 106.

non 1919 Calymmene pulchra BEYR.; Funkquist, p. 36, pl. 1, figs. 5, 6.

non 1922 Calymene pulchra Barr.; Freyberg, p. 245, pl. 4, fig. 6.

? 1931 Calymmene pulchra Barr.; Sun, p. 27, pl. 3, figs. 8a, b.

? 1951 Pharostoma parapulchra n. sp.; Kobayashi, p. 46, pl. 3, fig. 9.

1956 Pharostoma pulchrum pulchrum (BARRANDE, 1846); Snajdr (pars), pp. 504-5.

1960 Pharostoma pulchrum (Beyrich); Whittard p. 134, pl. 8, figs. 2-8.

? 1961 Pharostoma pulchrum (Beyrich); Curtis, p. 2.

1965 Pharostoma pulchrum mendax subsp. n.; Vanek, p. 30, pl. 2, fig. 10, pl. 3, figs. 6, 7, pl. 4, figs. 2-5.

1966 Prionocheilus pulcher (Beyrich); Dean (pars), p. 303.

non 1966 Prionocheilus pulcher pulcher (Beyrich); Destombes, p. 39, pl. 4, figs. 1-6.

1966 Pharostoma pulchrum vokovicense; Havlicek & Vanek, p. 26.

1966 Pharostoma pulchrum mendax VANEK; Havlicek & Vanek, pp. 53, 54, pl. 10, fig. 6.

1967 Prionocheilus pulcher mendax (Vanek); Dean, p. 313.

LECTOTYPE. Here selected; external mould of an incomplete cranidium; MB 303B.K.; Pl. 2, figs. 1, 2, 6.

Four syntypes of Beyrich were kindly sent to me by Dr. H. Jaeger from the collections of the Paläontologisches Museum, Humboldt Universität, Berlin. Professor P.C. Sylvester-Bradley was informed (in litt., 13.6.1972) by Dr. H. Jaeger that this material was used by Beyrich as a basis for his original figures (1846, pl. 2, figs. 6a-d). Specimens MB 501B.K. (internal mould cranidium) and MB 303B.K. (lectotype) were combined, perhaps also with other cranidia, and illustrated on pl. 2, figs. 6a, b; an internal mould of a free cheek, MB 502B.K./k190, was figured on pl. 2, fig. 6c and an internal mould pygidium, MB 264B.K./k191, on pl. 2, fig. 6d. The abbreviation B.K. refers to "Beyrich's Katalog"; some of his specimens were recatalogued at a later date and prefixed with the letter 'k'.

TYPE STRATUM AND TYPE LOCALITY. Letna Formation (lower Caradoc), Vesela, near Beroun, Czechoslovakia.

DIAGNOSIS. Preglabellar area and preglabellar field about one third and one eighth as long as glabella respectively. At median line anterior border is considerably swollen, in cross-section roll-like, rather broad, but narrows distinctly abaxially. Marked eye ridge is raised sharply above posterior part of fixed cheek. Anterior part of fixed cheek is somewhat distended.

DESCRIPTION. Glabella is just wider than long (sag.), generally parabolic in outline, not projecting anteriorly beyond fixed cheeks.

Behind central glabellar area occipital ring is transversely directed and equally wide (sag. & exs.), behind basal glabellar lobe it narrows to axial furrow, in lateral profile it is flat. Occipital furrow is very short (sag. & exs.) and sharply incised, somewhat broader on internal moulds. Lateral glabellar lobe 1p is subquadrate, both abaxial anterior and posterior corners are conspicuously angular, its abaxial margin is flat or at most weakly convex outwards. Lateral furrow 1p is moderately deep at axial furrow, trends inwards and gently backwards to deepen and bifurcate at inner, anterior corner of lobe 1p. Posterior branch continues in a broad arc backwards, turning more sharply inwards adaxially; a shallow depression connects this branch to occipital furrow. Anterior branch of furrow 1p is shorter than posterior, clearly traverses the neck of lobe 2p to meet furrow 2p. Within the fork of 1p furrow, side of central glabellar area is rather inflated. Lobe 2p is about half as large as 1p. Lateral furrow 2p is moderately deep, trends backwards more sharply than outer part of furrow 1p. Very short, indistinct (especially on lectotype cast) furrow 3p is sited low down on side of glabella and delimits a small, triangular shaped lateral lobe 3p which is confluent dorsally with central glabellar area. In outline, frontal lobe is evenly arched forwards to a greater or lesser extent. In lateral profile glabella falls gently from occipital furrow to furrow 2p, progressively more steeply thereafter to preglabellar furrow.

Beside occipital ring axial furrow is shallow and narrow, runs forward and outwards to lateral lobe 1p where it markedly expands (tr.) into the typical crescent shape with a steep but not deep outer wall; at lobe 2p it is narrow and abaxially convex. Anterior pit is opposite frontal lobe and situated on outer side of axial furrow. Some internal moulds display two very small, dorsally projecting stub-like features on the margins of the axial furrow, one is within the anterior pit, the other, which is somewhat larger, on the adaxial side of axial furrow where it meets lateral furrow 3p. Preglabellar furrow is not deep, slightly undercuts frontal glabellar lobe. Length (sag.) of preglabellar field varies from about one seventh to one tenth that of glabella; in lateral profile it is flat or gently convex. Anterior slope of shallow border furrow rises quite sharply to anterior border. The latter is rather puffy and sausage-shaped, in cross-section roll-like, widest at median line, unmistakeably narrowing (exs.) abaxially.

Posterior border constantly narrow to fulcrum, increases in width from here to suture line. On cast of lectotype the posterior border furrow is narrower (exs.) than posterior border, on internal moulds the border furrow appears about equal to or just wider than border. Abaxially posterior border and furrow connect with lateral border and weakly developed furrow which then run forwards to facial suture. Inner part of fixed cheek behind eye is rather flat, outer part slopes much more strongly downwards and backwards towards genal angle. Prominent eye ridge runs from front of palpebral lobe to anterior part of lateral glabellar lobe 2p, is then subparallel to axial furrow curving somewhat forwards to finish opposite lobe and furrow 3p. This ridge is distinctly raised above the level of the fixed cheek on its posterior side, much less so on its anterior side where it merges into the swollen, convex (exs. & tr.) preocular part of cheek. The latter falls steeply to anterior border and axial furrow, more gradually at its inner, anterior part to preglabellar field. Anterior branch of facial suture runs forwards in a mildly abaxially convex curve to anterior margin. Posterior branch is directed outwards and backwards from eye, more strongly so crossing lateral border furrow, finally runs exsagittally to posterior margin.

Palpebral lobe is centred opposite middle or anterior part of lateral lobe 2p, is not as long as that lobe, appears quite steeply upturned. Eye socle falls steeply to main part of free cheek which in its inner region is less steeply inclined than its outer region which is vertical. Lateral border furrow of internal mould is narrow, moderately deep, runs into anterior border furrow. Lateral border of mould is rolled over to meet doublure. From the material at hand, dorsal surface of genal spine is unknown but appears to be formed as a continuation of outer part of lateral border of free cheek. Doublure of free cheek is sharply reflexed upwards, narrows (tr.) a little from anterior to posterior sections of facial suture, then swings inwards to form ventral, enclosing cover to genal spine. On free cheek from juncture of lateral border and doublure about twenty eight stout spines project downwards and somewhat backwards, the most posterior ones are shortest, quickly increasing in length anteriorly but decreasing again near anterior facial suture and continuing onto rostral plate where they are less strongly developed. It is difficult to determine the abaxial limits of the rostral plate from internal moulds as connective sutures not preserved, but it would appear to have about ten spines.

Thorax has thirteen segments. Axis tapers posteriorly. Each axial ring bends forwards medially and stands well above pleural region. Each pleura is horizontal to weakly defined fulcrum then bends abruptly downwards at right angles. Posterior pleural band much wider (exs.) than anterior and is itself widest at axial furrow, narrowing abaxially.

Axial furrows of pygidium are well marked and converge posteriorly until fourth ring furrow after which they are subparallel, finally running inwards again, very quickly shallowing and barely meeting behind terminal axial piece. First four axial rings are deflected posteriorly near axial furrow, more sharply so on the fourth than the first. Axial rings become less convex (sag.) posteriorly and ring furrows not so strongly impressed. First four ring furrows are shallowest a little inwards from axial furrow, fifth and sixth do not reach axial furrow. Terminal axial piece has rounded outline, falls very steeply posteriorly to indistinct axial furrow. Six deeply incised pleural furrows traverse the pleural region which in its outer part slopes almost vertically to lateral margin. Distance between distal end of each pleural furrow and lateral margin gradually decreases from posterior to anterior part of pygidium. Interpleural furrows very weak, best seen, if at all, on inner part of pleural region. Where observed, posterior pleural band wider (exs.) than anterior.

Excluding furrows, whole surface of cranidium and pygidium covered with rather small closely spaced tubercles or granules, many of which are perforate. This type of ornamentation appears common to all Bohemian species of Pharostoma.

DISCUSSION. The authorship of Pharostoma pulchrum pulchrum is in dispute. Whittard (1960, p. 136) credited the taxon to Beyrich and not, as had formerly been widely accepted, Barrande because of Beyrich's prior publication. Vanek (1965, p. 30) disagreed with Whittard's conclusion on the grounds that it was in contradiction to Article 50 of the I C Z N, and retained Barrande as the author. It is clear from Beyrich (1846, p. 2) that the name Calymene pulchra was suggested to him by Barrande (Whittard 1960, p. 136) who had distinguished the species sometime before in his own collections. However, although Barrande invented the name, it was certainly Beyrich who wrote the description and thus met the conditions of availability. It is therefore Beyrich to whom the taxon must be attributed.

Dean (1967, p. 313) did not comment on Vanek's proposals and followed Whittard's usage though in error cites Emmrich, not Beyrich, as the author. Destombes (1966, p. 39) applied Beyrich's authorship as did Olin (1906, p. 58) Funkquist (1919, p.36) and Curtis (1961, p.) before him.

Beyrich's type specimens were believed lost (Dean 1967, p. 313) yet they are all extant and are refigured here for the first time. The lectotype previously chosen from Barrande's figured material (1852, pl. 19, fig. 2; NMP It 324, CD 1167) by Snajdr (1956, p. 505) is invalid (Article 74 (a) (i)) and I have consequently selected a cranidium from the syntypes of Beyrich. Moreover the specimen designated by Snajdr comes from the Zahorany Formation at Zahorany, yet all Beyrich's specimens are from the Letna Formation at Vesela, and they represent separate subspecies.

All former interpretations of Pharostoma pulchrum pulchrum will have to be reappraised as they were made without knowledge of the morphology of the true type specimens. It is probable that several of the previously recorded extra-Bohemian specimens, and for certain those from Scandinavia, have been mistakenly identified. The material of pulchrum pulchrum presently at hand from Czechoslovakia does not provide as much information as is desired regarding the total morphology and stratigraphical and geographical parameters of the subspecies within that country, and in order to impose more precise confines on this taxon it is intended to examine further collections. The rediscovery of the type specimens has provided the necessary prerequisite for this.

Pharostoma ranges from the Sarka to Bohdalec Formations (base of Llanvirn to top of Pusgillian) in Bohemia and hitherto three taxa have been erected from here: P. pulchrum, P. pulchrum vokovicense Snajdr, 1956 and P. pulchrum mendax Vanek, 1965. The occurrence of P. vokovicense has been dealt with above. The holotype of P. pulchrum mendax comes from the Letna Formation at Ded in the vicinity of Beroun, though the range of the subspecies extends from this typical horizon down to the Dobrotiva Formation (Vanek 1965, p. 32). As conceived on Snajdr's 'lectotype', 'P. pulchrum pulchrum (Barrande)' is present in the younger Vinice, Zahorany and Bohdalec Formations (Havlicek & Vanek 1966, pp. 54-56). The three taxa appear to be stratigraphically discrete.

The question arises as to which, if any, of these is synonymous with

P. pulchrum pulchrum (Beyrich, 1846). P. vokovicense is undoubtedly different. Vanek (1965) distinguished P. pulchrum mendax from the specimens he referred to 'P. pulchrum pulchrum (Barrande)' on no less than ten characters. These include a more subtriangular glabellar outline, more highly arched frontal glabellar lobe, shorter 2p lateral furrows, narrower (tr.) axial furrow around lobe 1p, a deep and broad occipital furrow, more distinct and shorter palpebral ridge, larger fixed cheeks, stronger and shorter genal spines which are more posteriorly divergent, a more convex (tr.) cephalon with stouter cephalic marginal spines, less distinct interpleural furrows, and better arched ribs on the pleural region of the pygidium. The material at my disposal does not allow me to assess the value of all these features though I have seen sufficient to be convinced that P. pulchrum pulchrum (Beyrich) also shows some of these differences from the stratigraphically later taxon (= 'P. pulchrum pulchrum Barrande' as used by Vanek and others), and that it is synonymous with P. pulchrum mendax Vanek. In particular the distinct nature of the eye ridge and anterior part of the fixed cheek (see description above) are the same in both pulchrum pulchrum and pulchrum mendax. What is more the type specimens of both are of the same age, Vanek listed Vesela (the type locality for P. pulchrum (Beyrich)) as one of the sites yielding pulchrum mendax, and indeed he placed Beyrich's specimens in the synonymy of his subspecies.

It is conceded that in the lectotype cast of pulchrum pulchrum (Beyrich) the frontal glabellar lobe and glabella are both more broadly parabolic in outline compared with the holotype of P. pulchrum mendax but as they are connected by specimens of intermediate morphology I have preferred to regard this variation as intraspecific. Moreover this dissimilarity may partly be accounted for by the differing states of preservation of the two cranidia, the holotype of P. pulchrum mendax being an internal mould. Even so, in this feature the lectotype cast of pulchrum pulchrum manifestly approaches the Pharostoma subspecies occurring in the Zahorany Formation.

The Pharostoma specimens assigned by Whittard (1960, p. 134) to P. pulchrum pulchrum (Beyrich) from the Lower Llanvirn Hope Shales were later referred by Havlicek & Vanek (1966, p. 26) to P. vokovicense but on the form of the anterior border they are without doubt distinct from Snajdr's species. The Shropshire material also exhibits small differences from typical Bohemian examples of pulchrum pulchrum and Dean (1967, p. 313) has noted that the single pygidium figured by Whittard (1960, pl. 18, fig. 8) shows a shorter subconical section to the anterior part of the axis. The Hope Shales cranidia are smaller, seem to have the palpebral lobe a little more anteriorly placed, and may have a few less marginal spines on the rostral plate, but in general they match well the Bohemian specimens and the differences are insufficient to warrant further separation. Contrary to the inference of Whittard (1960, p. 138) his material does possess an eye ridge.

Pharostoma parapulchrum Kobayashi, 1951 from the Llanvirn of south-west China was founded on one incomplete cranidium which was initially attributed to Calymene pulchra by Sun (1931, p. 27, pl. 3, figs. 8a, b). Unfortunately the anterior border of the holotype is missing but the rest of the cranidium is similar to pulchrum pulchrum from which it was distinguished by having a distinct eye ridge. This structure, however, is present in both taxa. Kobayashi's figure (1951, pl. 3, fig. 9) of P. parapulchrum appears to show a wider axial furrow beside lateral furrow 1p than is typical of pulchrum pulchrum, though in common with the Bohemian subspecies it seems to have a swollen anterior part to its fixed cheek. Kobayashi's species would benefit from redescription and reillustration, and more firm conclusions with respect to its taxonomic standing are dependent on this. For the moment it is tentatively placed in the synonymy of pulchrum pulchrum.

Pharostoma pulchrum was recorded by Delgado (1908, p. 106) from the Uralichas riberoi Slates of the Valongo area, Portugal. These rocks are of approximately upper Llanvirn or Llandeilo age (Curtis 1961, p. 3) and in the collections of the British Museum are specimens from this horizon and area obtained by Mr. J. T. Wattison. They are quite strongly distorted but nevertheless show strong affinities with the Bohemian stock and especially P. pulchrum. Delgado(1908, p. 57) also lists the species from the middle and upper Ordovician of the Bussacco Area, Portugal.

OCCURRENCE. With certainty from the Dobrotiva, Liben and Letna Formations (Llandeilo to lower Caradoc) of Bohemia and Hope Shales (Llanvirn) of the Shelve Inlier.

Pharostoma pulchrum subsp. nov. A

Plate 4, figs. 1, 2, 6, 9.

1846 Calymene Pulchra Barr.; Barrande (pars), p. 27

1852 Calym. pulchra. Barr.; Barrande (pars), p. 575, pl. 19, figs. 2, 3, 6 ? fig. 1.

1956 Pharostoma pulchrum pulchrum (BARRANDE 1846); Snajdr (pars), pp. 504-5.

1965 Pharostoma pulchrum pulchrum (Barrande, 1846); Vanek, pl. 3, figs. 3-5, pl. 4, fig. 1.

1966 Prionocheilus pulcher (Beyrich); Dean (pars), p. 303.

1966 Pharostoma pulchrum pulchrum (BARR.); Havlicek & Vanek, pp. 55, 56, pl. 11, fig. 13.

1966 Prionocheilus pulcher pulcher (Beyrich); Destombes, p. 39, pl. 4, figs. 1-6.

MATERIAL STUDIED. One well preserved but incomplete internal mould cranidium, DJS/139; coll Dr. L. Marek. Two ill preserved, internal moulds of incomplete individuals, NMP It324/CD 1167 and NMP It325/CD 1166.

OCCURRENCE. Zahorany Formation (middle Caradoc) at Lodenice (DJS/139) and Zahorany (NMP It324/CD 1167 and NMP It325/CD 1166). Also recorded from the Vinice and Bohdalec Formations (middle - upper Caradoc) of Bohemia (Havlicek & Vanek 1966, pp. 54-56) and upper Caradoc of Morocco (Destombes 1966).

DISCUSSION. This subspecies, of which I have only one serviceable specimen (DJS/139) at hand, has been previously referred to by Vanek (1965) and Havlicek & Vanek (1966) as '*P. pulchrum pulchrum* (Barrande, 1846)'.

The above cranidium (DJS/139) differs from *P. pulchrum pulchrum* (Beyrich) by having a much less swollen fixed cheek in front of the eye, a barely perceptible eye ridge which is not prominently raised above the level of the posterior part of the fixed cheek, and palpebral lobes which are more distant (tr.) from the axial furrow. An evaluation of the other differences of this subspecies from *P. pulchrum pulchrum*, (Beyrich) (= *P. pulchrum mendax*, Vanek 1965) which were given by Vanek (1966, p. 31), is not possible without access to more specimens. A full description and naming of the taxon will be deferred until then. The other two specimens available to me were originally figured by Barrande (1852, pl. 19, figs. 2 (NMP It324/CD 1167), 3 (NMP It325/CD 1166)), and one of them (NMP It324/CD 1167) was chosen as the 'lectotype' of '*P. pulchrum pulchrum*' (Barrande) by Snajdr (1956). They are too ill-preserved to convincingly display the differentiating cranidial characters outlined above, and previous illustrations of what is probably this subspecies are found equally wanting.

Pharostoma aff. P. denticulatum (Eichwald, 1860)

Plate 5, figs. 1-4.

MATERIAL. One incomplete cranidium; RM Ar10692; coll. G. Holm, 1880.

OCCURRENCE. Raniceps Limestone, Utby, Dalarna, Sweden. Thorslund (in Thorslund & Jaanusson 1960, p. 5) correlates this horizon with the lower Llanvirn of Britain.

DESCRIPTION. Glabella is as long as wide, parabolic in outline. Occipital ring narrows abaxially. Occipital furrow is moderately wide and deep between lobes 1p, more narrow and deep behind them. Lateral glabellar lobe 1p is slightly less than one third as wide as, and one third as long as, the glabella; it is subovate in outline, the long axis running exsagittally, and separated from central area of glabella by shallow depression. Furrow 1p is shallowest at axial furrow, swings inwards and backwards becoming deeper and wider around inside of lobe 1p; a short anterior branch trends forwards and inwards on adaxial side of lobe 2p where it shallows and connects with furrow 2p. At adaxial part of lateral furrow 1p, glabella is very mildly convex. Lobe 2p is subcircular in outline, distinctly separated from frontomedian lobe of glabella. Lateral furrow 2p trends inwards and at its inner part slightly backwards. Lobe 3p scarcely visible (especially on right side) due to coarseness of glabellar tubercles, its extremely small size and its situation low down on glabellar side. Furrow 3p is exceedingly faint, transversely directed. Frontal glabellar lobe has well rounded outline. In lateral profile glabella is gently convex from occipital furrow to furrow 2p, then falls progressively more steeply to preglabellar furrow.

Preglabellar furrow shallowest at anterolateral margins of frontal lobe, fractionally undercuts this lobe medially. Preglabellar field is about one sixth as long as glabella and gently convex along median line, more convex and longer exsagittally. Anterior border furrow of about same width (sag.) as occipital furrow. Anterior border projects forwards and upwards, is distinctly longer medially where it is drawn forward into a short, blunt, broad-based spine. Anterior margin runs inwards and forwards from facial suture.

The rest of the cranidium is missing.

Tubercles ornamenting the glabella and anterior border are very coarse. A few of these large tubercles are present on the inner extremity of fixed cheek where it runs into the preglabellar field. Fine pustules are scattered over much of the cranidium between the much larger tubercles.

DISCUSSION. Pharostoma denticulatum has not been revised since 1894 and it is therefore necessary to review the history of this species. It was originally described by Eichwald (1860, p. 1421) from the Orthoceratite Limestone of "Poulkowa", USSR, referred by him to Calymene, and the enrolled individual which he figured (1860, pl. 54, fig. 13) must be considered the type specimen. Schmidt (1894, p. 30, pl. 2, figs. 20-20c) later assigned denticulatum to Pharostoma, and basing his identification on specimens in the collections of Volborth and Eichwald, recorded its occurrence at "Pawlowsk und Pulkowa". Schmidt (1894, p.32) seems uncertain as to the age of the strata at these localities but preferred a level within Stage B_3 (uppermost part of the Oeland Series) or C_1 (lowermost part of the Viru Series). These Stages correspond approximately to the whole of the Llanvirn and lower Llandeilo Series of Britain (Williams in Williams, Strachan, Basset, Dean, Ingham et al. 1972).

The type specimen of P. denticulatum was not refigured by Schmidt, and his description of the species was based mainly on a well preserved individual in the Volborth Collection of his academy; I presume the latter specimen is the one he illustrates (pl. 2, figs. 20-20c) from Stage C_1 at Pawlowsk.

In 1907 (p. 57) Schmidt reaffirmed the occurrence of denticulatum in deposits of B_3 to C_1 age from the banks of the river "Popowka" near "Pawlowsk", and the banks of the river "Pulkowa" near "Pulkowo".

An upwardly inclined anterior border with a somewhat angular anterior margin which juts forwards medially, the lack of an intermediate lobe (= swelling on the side of the glabella at the inner end of lateral furrow 1p), the expansion of the axial furrow beside lobe 1p extending onto the fixed cheek, and rather coarse tubercles ornamenting the cranidium are the characters given by Schmidt (1894, pp. 13, 30-32) which combine to distinguish P. denticulatum. Although incomplete there is little doubt that the cranidium described above from the Raniceps Limestone belongs to Pharostoma; it is closely related to Eichwald's taxon and also P. nieszkowskii Schmidt, 1894 (see discussion of that species below) but appears more allied to P. denticulatum because of its rather coarse cranidial tubercles.

The holotype of P. denticulatum figured by Eichwald does not have any suggestion of a pointed anterior margin and certainly no definite spine as in the Swedish specimen but Schmidt, who apparently had better material than Eichwald, believed the former state to be characteristic of the species. Thus, as far as can be determined from the descriptions and illustrations of Schmidt and Eichwald, P. denticulatum does not have a distinct spine projecting from the border though some angularity of the anterior margin would appear typical. The Raniceps Limestone specimen is probably a separate species but at present I am deferring the establishment of a new taxon pending a modern revision of P. denticulatum.

Pharostoma aff. P. denticulatum represents the earliest member of the genus, if not the family, from Scandinavia and increases the hitherto known geographical range of Pharostoma in lower Ordovician rocks. Other species of Llanvirn age include P. parapulchrum Kobayashi, 1951 from China, P. vokovicense Snajdr, 1956 from Bohemia, and P. pulchrum from Britain. Only P. matutinum (Dean, 1966) from SW France is recorded from the Arenig. It is evident that the genus was widespread by early Ordovician times.

Pharostoma nieszkowskii Schmidt, 1894

Plate 5, figs. 5-7, 9; Plate 6, figs. 1-3, 5, 6.

1894 Calymmene Nieszkowskii n.sp.; Schmidt, p. 29, pl. 2, figs. 17, 18.

1907 Calymmene Nieszkowskii m.; Schmidt, p. 57.

1919 Calymmene pulchra BEYR.; Funkquist, p. 36, pl. 1, figs. 5-6.

1937 Pharostoma nieszkowskii Fr. Schmidt; Öpik, p. 22, pl. 15, fig. 4, pl. 16, text-figs. 1-3.

1960 Pharostoma nieszkowskii; Whittard, p. 137.

SYNTYPES. Schmidt (1894) illustrated three specimens, two of which were on the same piece of rock and figured together. His original of pl. 2, fig. 17 is a small, incomplete cranidium from the Museum at Tallinn ("Mus. Reval"), Estonia; pl. 2, fig. 18 shows the internal (ventral) view of two cranidia from the Nieszkowskii Collection of the Tartu (Dorpat) Naturalists Society ("Dorpater Naturforschungesellschaft").

TYPE STRATUM AND TYPE LOCALITY. The cranidium of Schmidt's pl. 2, fig. 17 is from the Viruan (Middle Ordovician) Kukruse Stage, Kukruse, Estonia and the two cranidia of pl. 2, fig. 18 from the Kukruse Stage at

Salla, near Erras, Estonia. The Kukruse Stage is regarded by Williams (in Williams et al. 1972, p. 8) as coincident with the range of Nemagraptus gracilis - that is from just below the middle Llandeilo to almost the top of the Costonian Stage, Caradoc Series.

MATERIAL AND OCCURRENCE. a) Two incomplete cranidia from Estonia; RM Ar34361 from Vanamoisa and RM Ar34406 from Kukruse. The latter specimen was collected by Dr. G. Holm in 1883; In his acknowledgements Schmidt (1894, p. 6) makes reference to an excursion with Holm and it seems probable it was obtained at this time.

b) An incomplete cranidium and pygidium from Tommarp, SE Scania, Sweden; IPLU LO 2955t, IPLU LO 2956t.

DIAGNOSIS. As for P. simile Thorslund, 1940 except the pygidium has only five axial rings and six pleural furrows.

DESCRIPTION. The cranidia at hand are not formally described as they are similar in most respects to those of P. similis which is treated fully below.

DISCUSSION. In 1937 Öpik refigured and briefly described Estonian material of P. nieszkowskii, though Schmidt's syntypes, if extant, still await re-examination. Two specimens from Scania (see material above) are best referred to this species, and were originally described and illustrated by Funkquist (1919, p. 36, pl. 1, figs. 5, 6) as Calymmene pulchra. Two cranidia available to me from Estonia match closely the descriptions and figures of Schmidt and Öpik and can with certainty be attributed to P. nieszkowskii.

Schmidt erected this species on the basis of a few cranidia and in characterizing the taxon he (1894, p. 6) stressed the upturned anterior border, median jutting forward of the anterior margin, 'intermediate lobe' on the glabella, well-marked eye ridge and variably sized surface tubercles. Most distinctive is the medially pointed anterior margin, a feature well shown by the three cranidia assigned herein to nieszkowskii.

Thorslund (1940, p. 146) believed the cranidium of P. simile to be identical with that of P. nieszkowskii except that the former is known to attain a larger size. From the material I have seen, the shape of the glabella and its lobes, amount of inflation on the side of the glabella at the inner end of furrow 1p, form of the axial furrow, distinct eye ridge, nature of the preglabellar field, anterior border and anterior margin, and the style of ornamentation are extremely alike in both species. The difference between them rests largely on Öpik's (1937, p. 22) description of a pygidium he assigned to P. nieszkowskii from the Kukruse Stage at Kohtla-Järve, which has only five axial rings and six pleural furrows. P. simile has from eight to ten axial rings and seven to eight pleural furrows. This distinction requires substantiating by the study of topotype pygidia of nieszkowskii, as Kohtla-Järve is not one of Schmidt's original localities, though Öpik (1937, pl. 16, fig. 2) has figured a well preserved cranidium of the species from there. The single pygidium from Scania(IPLU LO 2955t) is small and incomplete but has five or six pleural furrows and the same number of axial rings. For this reason I am referring the Scanian material to P. nieszkowskii rather than P. simile.

P. denticulatum (Eichwald, 1860) clearly resembles P. nieszkowskii in the form of its anterior margin but is distinguished, according to Schmidt (1894, pp. 12, 13, 31, 32), mainly by the absence of a distinct intermediate lobe, form of the dorsal furrow, and larger cranidial tubercles. Whittard (1960, p. 137) claims that in P. denticulatum the posterior margin of the palpebral lobe lies opposite the middle of the basal glabellar lobe and that the glabella has only two lateral lobes - presumably taking as evidence the illustrations of Schmidt (1894, pl. 2, fig. 20) and Eichwald (1860, pl. 54, fig. 13). The palpebral lobe of denticulatum does appear more posteriorly placed than in P. nieszkowskii, though the apparent absence of lateral lobe 3p may be on account of its small size and coarseness of glabellar tubercles. (see description of P. aff. P. denticulatum).

OCCURRENCE. Hitherto this species has only been recorded from the Kukruse Stage of the Viruan Series in Estonia. Schmidt's localities were given above. Öpik (1937) figures material from Kohtla-Järve, Vanamoisa, and Ubja, and Roomusoks (1970, p. 180) also records P. nieszkowskii from these localities.

The Scanian specimens are from the so-called "Ampyx" Limestone which lies between the zones of Nemagraptus gracilis and Dicranograptus clingani (Regnell and Hede 1960, p. 16, table 2.).

This species is possibly represented in the lower Chasmops Shale of the Oslo Region (see below). Material described herein as Pharostoma sp. indet. 1 from Västergotland shows some traits characteristic of P. nieszkowskii and is of a similar age to the Scanian specimens, though slightly younger than those from Estonia.

Pharostoma cf. P. nieszkowskii Schmidt, 1894

Plate 4, fig. 5; Plate 5, fig. 8.

DISCUSSION. Specimens that are compared with P. nieszkowskii, from the Lower Chasmops Shale of the Oslo Region, are discussed in the study of Middle Ordovician calymenids from Norway. Some of these specimens are refigured here to facilitate direct comparison with the Estonian material.

Pharostoma simile Thorslund, 1940

Plate 6, figs. 4, 7-12; Plate 7, figs. 1-10; Plate 8, figs. 1, 2, 4.

1940 Pharostoma similis n. sp.; Thorslund, p. 144, pl. 11, figs. 1-14.

1960 P. similis Thorslund, 1940; Whittard, p. 137.

HOLOTYPE. A well preserved cranidium; IPU Ar 2469; Pl. 6, figs. 4, 9.

TYPE STRATUM AND TYPE LOCALITY. Glacial erratics of the Lower Chasmops Limestone, Island of Ringsön, SE of Tvären, Sodermanland, Sweden. See Thorslund 1940, p. 110.

ADDITIONAL MATERIAL. The original specimens of Thorslund, together with several other cranidia, pygidia, and hypostomes, all of which are housed in the Institute of Palaeontology, Uppsala. One cranidium (RM Ar9150) from the Riksmuseum.

DIAGNOSIS. Preglabellar area about one third to two fifths as long as the glabella; preglabellar field about one fifth as long as the glabella. Anterior border moderately inclined forwards and upwards. Anterior margin somewhat pointed medially. Pygidium with eight to ten axial rings, seven to eight pleural furrows. The larger tubercles on the glabella and anterior border are mostly absent from the preglabellar field.

DESCRIPTION. Holotype cranidium just greater than twice as wide as long. Glabella is from 0.83 (in the smallest recorded specimen, IPU Ar2467) to 1.08 times (in the largest specimen, IPU Ar2468) as wide (tr.) as long. Occipital ring almost flat in profile, widest medially, of constant width (sag. & exs.) behind central glabellar lobe, narrows and swings backwards behind lobe 1p. Occipital furrow transversely directed and very narrow and sharply incised between lobes 1p, deepens and turns backwards abaxially. Lobe 1p just less than one third as wide as glabella, joined at anterior abaxial margin to lobe 2p. Furrow 1p is weak at axial furrow, runs inwards and backwards, deepens and widens as it does so, then turns sharply more backwards and shallows, finally curving inwards slightly. Faint depression connects this posterior branch of furrow 1p to occipital furrow. Short anterior branch of furrow 1p extends forwards over inner side of lobe 2p. Between anterior and posterior branches the side of central glabellar area is gently to moderately swollen. Lobe 2p is about half as long as 1p, well below the dorsal surface of and distinctly separated from central glabellar lobe. Lateral furrow 2p is wider (exs.) and deeper than furrow 1p at axial furrow, and trends inwards and more backwards than abaxial part of furrow 1p. Very small, triangular shaped lobe 3p is confined to the side of glabella, is confluent dorsally with median glabellar lobe and bounded anteriorly by short (tr.) faint furrow 3p. In outline frontal lobe is arched forwards but tends to be weakly indented at, and more so either side, the median line. In lateral profile dorsal surface of glabella stands well above lateral lobes and is horizontal from occipital furrow to furrow 2p, thereafter falling gently to preglabellar furrow.

Preglabellar furrow is shallowest at anterolateral margins of frontal lobe, somewhat deeper at indentations of frontal lobe. Preglabellar are about one third to two fifths as long as cranidium. Preglabellar field gently convex (sag.), more so in large specimens, and has a broad inflation separating anterior pit in axial furrow and deepening of preglabellar furrow abaxially from median line. Length of preglabellar field is about one fifth that of glabella. Anterior border furrow is rather broad (sag. & exs.) and shallow. Anterior border is moderately inclined forwards and upwards, just greater than two fifths as long as preglabellar area, and narrows abaxially from a point opposite (exs.) axial furrow. Anterior margin tends to be angular, projecting somewhat forwards medially. Axial furrow is expanded (tr.) into a crescent shape beside lobe 1p, becomes shallower, more narrow, and abaxially convex around lobe 2p, is wider again and trends forwards at side of 3p and frontal lobes.

On fixed cheek near axial furrow the posterior border is quite convex and narrow, becomes slightly wider and less convex near facial suture where it joins lateral border. Adaxially the posterior border furrow is deep and narrow; near facial suture it connects with shallow, weakly defined lateral border furrow. Palpebral lobe is preserved on only one specimen (IPU Ar2467) and is very steeply upturned. Eye ridge runs forwards, inwards and downwards into axial furrow at, or in front of, furrow 3p and behind anterior pit. From opposite lateral lobe 1p to fulcrum fixed cheek is gently convex (tr.), but slopes strongly downwards from fulcrum to genal angle. In front of palpebral lobe the fixed cheek is convex and slopes steeply towards anterior border furrow; it also extends forwards and inwards passing into preglabellar field. On fixed cheek between axial furrow and posterior part of palpebral lobe, there is a distinct swelling. Posterior branch of facial suture bends outwards and progressively more backwards to posterior margin.

Thorslund adequately described the free cheek, hypostome, thorax and pygidium but the following additional comments apply. Marginal spines on free cheek originate from junction of lateral border and its doublure. The latter becomes markedly broader at genal angle. A well developed eye socle is present. Rostral plate unknown. There do not appear to be any inflated maculae on hypostome though, in the position which these normally occur, the median furrow slightly bifurcates.

Whole cranidium except deepest parts of furrows is covered with a ground mass of fine pustules, superimposed on which are tubercles of varying size. Some specimens appear to have a line of medium-sized tubercles on posterior part of preglabellar field following adaxial extension of fixed cheek. As a whole the preglabellar field lacks the larger tubercles found on the glabella and anterior border. On the anterior part of fixed cheek, running diagonally outwards from near anterior pit, are several faint, discontinuous ridges. These ridges are also weakly indicated on free cheek, trending abaxially from posterior part of eye socle. On one pygidium (IPU Ar2476) there is a possible paired arrangement of tubercles on each axial ring. Hypostome is covered with very fine pustules.

DISCUSSION. The cranidium of _P_. _simile_ is described for the first time and differences have been noted between the smallest (IPU Ar2467) and largest (IPU Ar2468) specimens which probably represent a true change in morphology during growth. The smallest specimen differs from the largest in the following respects. Between lateral lobes 1p the occipital furrow is less strongly defined; the glabella is relatively narrower across the basal lobes (compared to the width of the frontal lobe or the glabellar length); lateral lobe 1p is less subquadrangular and its outer margin is more straight, not abaxially convex; the frontal lobe is not so strongly arched forwards; the preglabellar field is much less convex (sag.) and the mid-point of the eye is opposite lobe 3p, not the middle of lobe 2p.

The smallest pygidium (IPU Ar2476) of _simile_ shows weak, but definite interpleural furrows. A specimen twice as large (IPU Ar2478) has, at most only the vaguest suggestion of these furrows. A similar trend during ontogeny towards a decrease in the impression of the interpleural furrows has been observed in _Flexicalymene jemtlandica_ Thorslund, 1940 from the Upper _Chasmops_ Limestone of Norway.

An isolated specimen of simile from Jämtland (RM Ar9150) displays a more narrow (sag. & exs.) anterior border than specimens from the type locality, but in all other characters it is the same and falls within the range of variation here allowed to this species.

The faint, discontinuous ridges on the anterior part of the fixed cheek and the free cheek may be regarded as cephalic caeca. Öpik (1961, p. 410) has described far better examples of caeca in Cambrian redlichiids and olenellids and believed them to represent the external expression of the internal alimentary system. He also noted that in Ordovician and younger trilobites this "alimentary prosopon" is rarely observed, and that in specimens which have retained the cuticle a "thin smooth test preserved in limestone yield(s) the best results". The surface tubercles in P. simile somewhat obscure the ridges, the cuticle appears thin, and the specimens are well preserved in limestone. Comparable ridges have been recorded in a similarly preserved new species of Pharostoma from the Upper Chasmops Limestone of the Oslo Region, Norway.

A comparison of P. simile with P. nieszkowskii is made in the discussion of that species. P. foveolatum (Törnquist, 1884) from the Kullsberg Limestone of Dalarna, Sweden and the new Norwegian species both differ in having a much longer preglabellar field and preglabellar area, together with a less angular anterior margin. In addition, foveolatum has eleven to thirteen axial rings and eleven to twelve pleural furrows on its pygidium; the Norwegian species has a flat or mildly concave upwards preglabellar field in lateral profile, and there is no distinction in size between the tubercles on its preglabellar field and those on its glabella and anterior border.

P. simile and P. pulchrum (Beyrich, 1846) are the only taxa examined which have provided free cheeks with well preserved lateral marginal spines. Although the two species are easily separated on many other characters it is noteworthy that the disposition of these spines is different in both and that they provide a useable discriminating feature. In P. simile short portions of the lateral margin of the free cheek are clearly perceptible separating the spines. In P. pulchrum the spines have their proximal ends touching each other and they are more numerous.

OCCURRENCE. All specimens except one come from the type stratum and locality. A single cranidium (RM Ar9150) was obtained from a loose block of Ordovician age, at Ytterhallen, Jämtland.

Pharostoma foveolatum (Törnquist, 1884)

Plate 8, figs. 5-11; Plate 9, figs. 1-3, 5-7; Plate 10, fig. 2.

1884 Calymene foveolata n. sp.; Törnquist, p. 43, pl. 1, fig. 45 (holotype).

1894 Calymene (Pharostoma) foveolata; Schmidt, p. 25.

1925 Pharostoma foveolata Törnquist; Warburg, p. 160, pl. 4, figs. 11-20.

1940 Pharostoma foveolata (Törnquist); Thorslund, p. 146.

1960 P. foveolata (Törnquist); Whittard, p. 137.

HOLOTYPE. A well preserved internal mould of an incomplete cranidium; SGU unnumbered; Pl. 8, figs. 5-8.

TYPE STRATUM AND TYPE LOCALITY. Kullsberg (Lower Leptaena) Limestone, Furudal, Dalarna, Sweden. The Kullsberg Limestone is recorded by Jaanusson (1963, p. 20, fig. 3) as straddling the boundary between the zones of Dicranograptus clingani and Diplograptus multidens.

ADDITIONAL MATERIAL. Several incomplete cranidia and pygidia in the Institute of Palaeontology, Uppsala, one pygidium in the SGU and one cranidium in the Riksmuseet.

DIAGNOSIS. Preglabellar area is from just less than a half to almost three fifths as long as glabella. Preglabellar field is from about one third to almost a half as long as glabella and convex upwards in lateral profile. Anterior border is steeply inclined, less than one quarter as long as preglabellar area. Pygidium has eleven to thirteen axial rings, eleven to twelve pleural furrows. (Slightly emended from Warburg 1925, p. 155).

DESCRIPTION. Warburg's description of this species (1925, p. 160) is most detailed and little need be added here. The two impressions in the preglabellar furrow, one either side the median line, which broadly indent the outline of the frontal glabellar lobe were noted by her. Although not so obvious, this lobe is also a little flattened (tr.) at its apex and the preglabellar furrow slightly steeper at this point (see holotype).

One very well preserved pygidium (IPU Ar465) from Skalberget, has a conspicuous node in the axial furrow behind the terminal axial piece. However, in all other respects it is in accordance with previously described pygidia of P. foveolatum and a cranidium (IPU Ar466) which is referred to this species has been found at the same locality.

DISCUSSION. This most unusual species is characterized by a very long (sag.), convex preglabellar field and the great number of axial rings and pleural furrows on its pygidium.

The smallest known specimen (the holotype) has a preglabellar field almost one third as long as the glabella though in a much larger specimen (IPU Ar469) it is just less than a half as long, which suggests there is a relative increase of this feature during ontogeny (Warburg 1925, p. 162).

The Silurian species Spathacalymene nasuta (Ulrich, 1879) and 'Spathacalymene' linguata Tomczykowa, 1970 both have a long preglabellar area and correspondingly long rostral plate. Neseuretus parvifrons (McCoy, 1851) from the Arenig Series of Wales also has a long preglabellar area but in this case it is combined with a sagittally extended anterior border to its hypostome (Whittington 1966, p. 502); its rostral plate is of normal length. Elongation of either the rostral plate or anterior border of the hypostome, in species with a long preglabellar area, may be explained by a need to maintain the anterior wing process of the hypostome in contact with the ventrally directed boss formed by the anterior (hypostomal) pit of the cranidium. Neither the rostral plate nor hypostome of P. foveolatum is known though one might expect similar changes to occur.

The more impressed parts of the preglabellar furrow - at the median line and particularly either side this line - may represent areas of muscle attachment, but they are not the same as those Öpik (1937, p. 23, fig. 2c) recorded in front of the glabella in P. nieszkowskii.

Pharostoma foveolatum is comparable to only one other species of the genus in the unusual length of its preglabellar field and preglabellar area - P. narinosum sp. nov. (see below). The new species is distinguished by a relatively longer, less upturned anterior border and a flat or gently concave upwards preglabellar field. Also some specimens of foveolatum show obtusely pointed tubercles on the anterior margin of the cranidium (IPU Ar469) which are unknown in P. narinosum. A comparison of P. foveolatum with P. simile will be found under the latter species. It is likely simile gave rise to foveolatum.

The pygidium of P. foveolatum exhibits far more axial rings and pleural furrows than is known in any other calymenid and its gross morphology is not unlike that of Chasmops. Warburg (1925, pl. 11, figs. 23, 24) figures a pygidium of Chasmops macrourus Sjögreni from the Kullsberg Limestone at Kullsberg, but it has even more axial rings and pleural furrows (sixteen to eighteen of both), is sagittally longer, and displays interpleural furrows.

OCCURRENCE. All specimens to date come from the Kullsberg Limestone of Dalarna, Sweden. Skalberget may be added to the localities of Kullsberg, Furudal, Amtjarn and Sinksjon given by Warburg. Only the holotype is known from Furudal; the majority of specimens are from Kullsberg.

Pharostoma cf. P. foveolatum (Törnquist, 1884)

Plate 9, fig. 4.

DISCUSSION. Two small, incomplete specimens from the Mjøsa Limestone of the Oslo Region are close to P. foveolatum but cannot be assigned with certainty to this species. A full discussion is given in the study of Middle Ordovician calymenids from Norway. Specimens are refigured here for comparison with the Kullsberg Limestone material.

Pharostoma narinosum sp. nov.

Plate 10, figs. 1,6.

DISCUSSION. A full description and discussion of this new species from the Upper Chasmops Limestone of the Oslo Region will be found in the account of Middle Ordovician calymenids from Norway.

<u>Pharostoma</u> sp. indet. 1.

Not figured.

1948 <u>Pharostoma</u> sp.; Thorslund, p. 363, pl. 21, figs. 4-6.

1960 <u>Pharostoma</u> sp.; Whittard, p. 138.

1964 <u>Pharostoma</u> sp.; Jaanusson, p. 12, table 3, p. 68.

MATERIAL. Is poorly preserved and fragmentary and consists of a cranidium, pygidium and two free cheeks; IPU, unnumbered in Thorslund's 1948 paper.

OCCURRENCE. From a depth of 64.24 - 64.29m in the Middle Ordovician rocks of the Kullatorp Boring, Kinnekulle Västergotland, Sweden. This level is within the Viruan Skagen Limestone, between the zones of <u>Nemagraptus gracilis</u> and <u>Dicranograptus clingani</u> (Jaanusson 1964, p. 8, table 1).

DISCUSSION. The present writer has not examined this material and it seems (from the plates) too ill preserved to identify with confidence at the specific level though I share the view of Thorslund (1948, p. 363) that it is related to <u>P. nieszkowskii</u> Schmidt, 1894. Thorslund described the cranidium as "broadly rounded in front" but the outline of the anterior margin appears to be somewhat angular at the median line (Thorslund 1948, pl. 21, figs. 4a, 4b). This feature is characteristic of both <u>P. nieszkowskii</u> and <u>P. simile</u>, as is the moderately upturned anterior border. The length of the preglabellar field seems about the same as in these species or perhaps somewhat shorter. In having only five axial rings and five pleural furrows the pygidium is more akin to <u>P. nieszkowskii</u> than to <u>P. simile</u>.

Pharostoma sp. indet. 2.

Plate 8, fig. 3.

? 1960 Pharostoma sp. indet.; Jaanusson, p. 230.

MATERIAL. One incomplete cranidium with the remains of nine thoracic segments; RM Ar23608.

OCCURRENCE. Dalby Limestone (= Zone of Nemagraptus gracilis; Jaanusson 1973, p. 20, fig. 3), Böda Hamn, Öland.

DESCRIPTION. Lateral lobe 1p is large, subquadrate, joined to outer, posterior corner of lobe 2p. Lateral furrow 1p is directed inwards and backwards, bifurcates into long posterior and short anterior branches; posterior branch almost completely divorces lobe 1p from central area of glabella; anterior branch is sharply incised and almost meets lateral furrow 2p to leave only a narrow neck connecting lobe 2p to frontomedian glabellar lobe. Lobe 3p extremely small; furrow 3p very weak. Outline of frontal glabellar lobe (reasonably preserved only on the right side) from most anterior part of axial furrow to median line is rather straight, trending inwards and forwards to median line.

DISCUSSION. The fragmentary nature of this specimen militates against precise determination. The whole of the preglabellar area, important for specific discrimination, has been destroyed but the obliquely flattened outline to the anterolateral margin of the frontal lobe strongly suggests it belongs with the P. simile - P. foveolatum group of species.

Pharostoma oelandicum Angelin, 1854

Plate 10, figs. 3, 4, 5, 7.

1854 Pharostoma ? Oelandicum n. sp.; Angelin, p. 62.pl.33,figs.15,15a.

? 1861 Calymene Pediloba n. sp.; Roemer, p. 74, pl. 8, fig. 6.

? 1894 Calymmene pediloba F. Röm; Schmidt, p. 26, pl. 2, figs. 12-16.

1894 Pharostoma oelandicum Ang.; Schmidt, p. 28.

? 1894 Cal. (Pharostoma) oelandicum Ang.?; Schmidt, p. 29, pl. 2, fig. 19.

1925 Ph. oelandicum ANG.; Warburg, p. 160.

? 1928 Calymmene (Pharostoma) oelandica ANG. sp.; Kummerow, p. 9.

1940 Pharostoma oelandicum ANG.; Thorslund, p. 146.

1960 P. oelandicum (Angelin); Whittard, p. 138.

HOLOTYPE. An incomplete cranidium; RM Ar2285; Pl. 10, figs.3,4,5,7.

TYPE STRATUM AND TYPE LOCALITY. Angelin originally recorded the species from his layer C on Öland. The youngest outcrop on this island is of the Dalby Limestone which approximates to the lower two thirds of the Nemagraptus gracilis Zone (Jaanusson 1973, p. 20, fig. 3), or about middle and upper Llandeilo in age. Schmidt (1894, p. 28) strongly doubted the horizon given by Angelin as he considered P. oelandicum probably synonymous with specimens he referred to Pharostoma pedilobum (Roemer, 1861) which occur in much younger strata, Stages E and F_1 (= middle Caradoc to middle Ashgill), from the Estonian Ordovician. Schmidt turned to Lindström for advice and both were convinced that the holotype of Angelin's species came from glacial erratics of the Macrourus Limestone, which is of Dicranograptus clingani Zone age - approximately middle and upper Caradoc (Thorslund in Thorslund & Jaanusson 1960, p. 5). These boulders were transported to Öland by a westerly moving ice flow (Jaanusson 1960, p. 209).

ADDITIONAL MATERIAL. None.

DIAGNOSIS. Moderately arched outline to frontal glabellar lobe. Preglabellar area and gently convex (sag.) preglabellar field are, respectively, just less than one quarter and about one tenth as long as glabella. Anterior border furrow rather broad and very shallow. In outline anterior margin is broadly convex forwards. Mid-point of palpebral lobe is opposite (tr.) centre of lobe 2p.

DESCRIPTION. Glabella just longer (sag.) than wide. Occipital ring half as wide (exs.) at axial furrow than at median line. Occipital furrow very narrow (sag. & exs.), sharply incised and transversely directed across central glabellar area, curves backwards abaxially. Lobe 1p is about one third as wide and two fifths as long as glabella, and joined to posterior abaxial corner of lobe 2p. Outer margin of lobe 1p is almost straight, anterior and posterior abaxial corners are rather angular. Lateral furrow 1p is shallow at axial furrow, trends inwards and backwards, becomes wider (exs.), deeper and divides into two branches below swelling of median glabellar lobe; posterior branch turns more backwards, anterior branch runs forwards to join with furrow 2p. Lobe 2p is about half as long as 1p. Lateral furrow 2p trends inwards and backwards. Lobe 3p is very small, only just visible in dorsal view, widest (exs.) adaxially due to convergence of lateral furrows 2p and 3p towards axial furrow. Furrow 3p runs transversely.

Preglabellar furrow about same width (sag.) as occipital furrow, much narrower than anterior border furrow, shallowest at junction with axial furrow. Preglabellar field is about one tenth as long as glabella, gently convex, falls down to broad (sag.), very shallow anterior border furrow. Anterior border projects forwards horizontally; anterior margin is broadly arched in outline, much more so than frontal lobe.

Axial furrow is mostly destroyed, though its expansion around (the left) lobe 1p can be seen; at lateral lobe 3p it receives the end of a weak eye ridge. Anterior pit situated below side of frontal lobe. Palpebral lobe is about equal in length to lobe 2p and is centred opposite (tr.) that lobe. Anterior part of fixed cheek slopes steeply forwards (exs.) to anterior border furrow, and abaxially runs into narrow pre-glabellar field. Anterior branch of facial suture runs almost directly forwards.

Whole cranidium except furrows covered with tubercles of various sizes, but none are very coarse.

DISCUSSION. This species is revised for the first time. Angelin offered only one line of description and his illustrations were rather small. The resemblance of P. oelandicum to taxa found at and above the Zone of D. clingani supports the arguement of Schmidt (see type stratum and locality) that it occurs above the layer C of Angelin.

In the form of its preglabellar field and horizontal attitude of its anterior border, oelandicum is closely allied to the Ashgill species P. leptaenarum (Törnquist, 1884), but leptaenarum has more anteriorly placed eyes (a line connecting their mid-points running through the outer end of lateral furrow 2p), and a more bluntly rounded outline to the frontal glabellar lobe. A further difference may be the length of the anterior border compared to that of the preglabellar field. It is difficult to determine in Angelin's holotype where the division between these two features lies, as the anterior border furrow is rather broad (sag.), though the anterior border seems longer than the preglabellar field. Specimens of P. leptaenarum figured herein (Pl. , figs. and by Dean (1971, pl. 18, fig. 11) show the preglabellar field to be longer than the anterior border. Also the preglabellar field is about one sixth as long as the glabella in leptaenarum but only one tenth as long in oelandicum.

P. obtusum (McCoy, 1846) differs from oelandicum in the same characters as leptaenarum, in addition to which it has spines on the anterior border.

P. rarum Cooper & Kindle, 1936 from the Ashgill of Quebec and a species referred to as Pharostoma sp. 'A' from the Upper Chasmops Limestone of the Oslo Region, are similar to P. oelandicum in having a very short preglabellar field. Both are distinguished by a more steeply inclined anterior border, more anteriorly positioned palpebral lobe, slightly coarser glabellar tubercles, and a less strongly arched outline to the frontal lobe.

Schmidt (1894, p. 28) seemed convinced that P. pedilobum (Roemer, 1861) was a junior synonym of P. oelandicum, having studied plaster casts of both type specimens, yet he continued to describe his material under pedilobum and questionably placed oelandicum in its synonymy. Unfortunately he did not refigure the holotype of P. pedilobum, which had been inadequately described and illustrated by Roemer (1861, p. 74, pl. 8, fig. 6). This holotype, which was collected from the glacial erratics of Silesia and at the time of Schmidt's account apparently housed in the Wroclaw (Breslau) Geological Museum, Poland, is still in need of re-examination. The specimens referred by Schmidt (1894, pl. 2, figs. 12-16) to "Cal. (Pharostoma) pediloba" from Stage E of the Estonian Ordovician match closely the holotype of P. oelandicum in glabellar and preglabellar morphology and position of the eye; he did not illustrate any material from Stage F_1. The specimen Schmidt (1894, pl. 2, fig. 19) figured as "Cal. (Pharostoma) oelandicum Ang. ?" was collected from N German erratics at Eberswalde by Remele, who originally recorded it (1885, p. 21) as P. oelandicum from the Macrourus Limestone. Kummerow (1928, p. 9) lists P. oelandicum from Macrourus Limestone erratics of the N German Plain, but failed to depict his examples. All of this material is tentatively assigned to oelandicum.

In some respects _P. oelandicum_ is intermediate in morphology between middle and upper Ordovician Scandinavian species. The outline of its frontal lobe is more reminiscent of _P. nieszkowskii_ than _P. ornithoreos_ sp. nov., but the reverse is true when considering the overall form of its preglabellar area.

OCCURRENCE. At present known only from the type stratum and locality. As far as I am aware the _in situ Macrourus_ Limestone has not produced any other specimens. Material referred to in the discussion from erratics of the N German Plain and Stages E and F_1 of the Estonian Ordovician may belong with this species.

Pharostoma ornithoreos sp. nov.

Plate 11, figs. 1-7.

DERIVATION OF THE NAME. Diminutive of the Greek, _orneon_, bird, and _oreos_, hill, pertaining to the type stratum and type locality.

HOLOTYPE. Incomplete cranidium; BM It8931; coll. S.F. Morris, 1965; Pl. 11 , figs. 1, 2, 6, 7.

TYPE STRATUM AND TYPE LOCALITY. Birdshill Limestone, Pusgillian Stage, Ashgill Series, quarry 200 yards NW of Birdshill Farm, one and a half miles WNW of Llandeilo, Carmarthenshire, S Wales.

ADDITIONAL MATERIAL. Two incomplete cranidia, BM It8930, BM It 8934; one incomplete external mould cranidium, BM It8933.

DIAGNOSIS. Preglabellar area and preglabellar field about one third and one seventh as long as the glabella, repectively. Preglabellar field moderately convex (sag.), fractionally shorter (sag.) than the broad, gently upturned anterior border. Anterior margin very weakly cuspidate. Frontal glabellar lobe bluntly rounded. Palpebral lobe sited opposite (tr.) middle or anterior part of lateral glabellar lobe 2p.

DESCRIPTION. Glabella is longer than wide. Lateral glabellar lobe 1p is less than one third as wide as glabella, elongated exsagittally, subrectangular in outline but more subtriangular in smaller specimens. Lateral furrow 1p is weakest at axial furrow, deepest around anterior adaxial margin of 1p lobe where it is obtusely angled, continues posteriorly as very shallow depression across neck of lobe 1p to occipital furrow. Lateral lobe 2p is about half as long as lobe 1p and as long as it is wide. Lateral furrow 2p is directed inwards and backwards to end opposite (exs.) anterior corner of lobe 1p. Lateral lobe 3p is rather small, triangular in outline, widest adaxially, present only on glabellar side, demarcated anteriorly by weak lateral furrow 3p. Bluntly outlined frontal glabellar lobe is subrectangular shaped and about three-fifths as wide as glabella. Frontomedian glabellar lobe narrows gradually towards occipital furrow, in profile stands well above lateral glabellar lobes and falls evenly from lobe 2p to preglabellar furrow.

Axial furrow is narrow next to occipital ring, widest and crescent-shaped beside lobe 1p, abruptly narrows again before reaching furrow 1p, is abaxially convex around lobe 2p, at side of lobe 3p and frontal lobe it runs more or less straight forwards and merges into preglabellar furrow. On outer side of axial furrow and half-way along the side of the frontal lobe is a shallow anterior pit. Between this pit and furrow 2p the end of a weakly developed eye-ridge runs into axial furrow.

Preglabellar area is about one third as long as glabella. Preglabellar furrow is uniformly shallow around frontal glabellar lobe. Preglabellar field is about one seventh as long as glabella, not quite as long as anterior border, and moderately convex (sag.). In front of glabella, anterior border furrow is very shallow, becomes better marked towards facial suture. Dorsal surface of anterior border is mildly convex, gently upturned, and rather broad (sag. & exs.). Outline of anterior margin is not smoothly convex forwards but weakly cuspidate. One cusp is sited on the median line, one opposite (exs.) each axial furrow, and on the holotype a fainter one is indicated opposite the left palpebral lobe. Each cusp is very obtusely pointed, not projecting far beyond general outline of anterior margin.

Abaxial posterior part of cheek is missing. Posterior border near axial furrow is tightly convex. Posterior border furrow very narrow (exs.). Palpebral lobe steeply upturned, on holotype its mid-point is situated opposite centre of lobe 2p, on another, slightly smaller specimen (BM It8930) it is opposite anterior part of this lobe. Anterior part of fixed cheek slopes steepest in direction of facial suture which is directed forwards and slightly outwards. Fixed cheek progresses adaxially in front of glabella and grades into preglabellar field.

Rostral plate, hypostome, thorax and pygidium unknown.

DISCUSSION. P. ornithoreos accords well with other upper Ordovician species in glabellar shape and the outline of its frontal glabellar lobe. Specific discrimination within this group is largely dependent on differences in the preglabellar area such as the form, inclination and length of the anterior border, and the nature of the preglabellar field. Prior to this study three species of Pharostoma have been established from strata of Ashgill age - P. obtusum, P. leptaenarum and P. rarum. The Welsh cranidium does not fall readily into any of these taxa and, occurring at the base of the Ashgill, is possibly earlier in age than any of them. Just four cranidia of ornithoreos are available, one of which (BM It8930) does not possess a well preserved anterior margin, but the other specimens display the same distinct type of preglabellar area which provides the basis for its recognition as a separate species.

As distinct from the new taxon, P. leptaenarum and P. obtusum have a horizontally protruding anterior border which is narrower than the preglabellar field. For example in the holotype of P. leptaenarum, the anterior border is only one third the width of the preglabellar field. Other specimens of leptaenarum do not show quite such a narrow border, but it is never as wide in this species as in ornithoreos. One of the Birdshill Limestone specimens (BM It8930) appears to have its preglabellar field wider than the anterior border but the reasons for this are twofold. Because this cranidium is embedded in a coarsely crystalline limestone it proved difficult to clean without fracturing, and so the anterior margin has been partly destroyed during preparation. Secondly, most of the preglabellar area is internal mould and where this is the case the preglabellar field becomes relatively longer at the expense of the anterior border (see also the discussion of P. leptaenarum).

The anterior margin also distinguishes these three species; that of P. obtusum is inferred to have forwardly directed spines and that of P. leptaenarum lacks any projections, both of which differ from the weakly cuspidate outline in P. ornithoreos. The short spines of P. obtusum are symmetrically arrayed on the anterior border and are in the same positions as the more obtusely-based cusps in the new species. It is probable that this arrangement is an inherited characteristic.

The palpebral lobe on the holotype of P. ornithoreos, lies opposite the centre of glabellar lobe 2p whereas in P. leptaenarum and P. obtusum it opposes the lateral furrow 2p. Of the other three Welsh specimens one (BM It8934) has both palpebral lobes destroyed, and the other two cranidia (BM It8930, BM It8933) have only one preserved, and in each case its mid-point is in line with the anterior part of lobe 2p. P. ornithoreos seems to have more posteriorly sited eyes though it would be useful to have extra cranidia from the Birdshill Limestone to substantiate this belief.

As noted in the discussion of P. leptaenarum, P. rarum would greatly benefit from revision, but it appears to have a much shorter preglabellar area (about one fifth as long as the glabella compared to one third in ornithoreos and lacks the characteristic anterior margin of the Welsh species.

P. oelandicum has a shorter preglabellar area and preglabellar field, smoothly outlined anterior cranidial margin, more strongly arched (in dorsal view) frontal lobe, and narrower (tr.) central glabellar area between lateral glabellar lobes 1p.

A single ill-preserved cranidium (BM unnumbered) of Pharostoma from the slightly younger (Cautleyan) Sholeshook Limestone near Haverfordwest may belong to ornithoreos. The length of the anterior border to preglabellar field is about the same and the median and abaxial (opposite axial furrow) cusps are present. The frontal glabellar lobe is less blunt though the oblique distortion suffered by the largely exfoliated specimen probably gives rise to this effect.

Pharostoma sp. A.

Plate 11, fig. 10.

DISCUSSION. Two small cranidia from the Upper Chasmops Limestone of the Oslo district are quite well preserved but unfortunately incomplete. The species is allied to later Ashgill forms and a full discussion is given in the study of Middle Ordovician Norwegian calymenids.

Pharostoma sp. B.

Plate 11, fig. 9.

DISCUSSION. Incomplete and distorted cranidia from the Upper Chasmops Shale of the Oslo district are close to Pharostoma sp. A, but clearly show a fringe of forwardly directed spines on the anterior border. The species is further compared with Pharostoma sp. A and other taxa in the chapter on Norwegian Middle Ordovician calymenids.

Pharostoma obtusum (McCoy, 1846)

Plate 12, figs. 1, 2, 4-6, 11, 13.

1846 Otarion obtusum; McCoy, p. 54, pl. 4, fig. 6.

1925 Pharostoma Leptaenarum Törnquist; Warburg (pars), p. 155, pl. 4, figs. 2, 5-9, ? figs. 3, 4.

1925 Ph. obtusa McCoy; Warburg, p. 423.

1960 Pharostoma obtusum (M'Coy); Whittard, p. 137.

1965 Pharostoma obtusum (M'Coy, 1846); Whittington, p. 55, pl. 16, figs. 1-3, 6.

1965 Pharostoma cf. obtusum (M'Coy, 1846); Whittington, p. 56, pl. 16, figs. 4, 5, 7, 8.

1971 Prionocheilus obtusus (McCoy); Dean, p. 42, pl. 18, figs. 2, 4-6, 8, 10, 12-15, pl. 19, figs. 5-8, 10, 12.

HOLOTYPE. Incomplete cranidium; NMI unnumbered; Sir Richard Griffith Collection; not figured herein, figured McCoy 1846, pl. 4, fig. 6, Whittington 1965, pl. 16, figs. 1-3, 6 and Dean 1971, pl. 18, figs. 10, 12, 13.

TYPE STRATUM AND TYPE LOCALITY. Chair of Kildare Limestone, Chair of Kildare (exact locality unknown), south-west of Dublin, Eire. The Kildare Limestone is of late Ashgill, middle Rawtheyan to lowermost Hirnantian, age (Williams in Williams et al. 1972, p. 57).

ADDITIONAL MATERIAL. At least seven cranidia from Kallholn (Riksmuseet collections), in addition to the material mentioned and figured by Warburg (1925), Whittington (1965), and Dean (1971) from Sweden, N Wales and Eire respectively.

DIAGNOSIS. Frontal lobe bluntly rounded. Preglabellar area about one quarter to three tenths as long as glabella. Preglabellar field gently convex (sag.), about one fifth to one seventh as long as glabella. Anterior border projects forwards horizontally. Anterior margin of cranidium has a fringe of short, forwardly directed spines. Mid-point of palpebral lobe is opposite outer end of lateral glabellar furrow 2p.

DESCRIPTION. The description of Whittington (1965) is comprehensive and little need be added here. The positions on the anterior border where the forwardly projecting spines occur are as follows: One on the median line, one opposite (exs.) each lateral margin of the frontal lobe and a less obvious one opposite each palpebral lobe near where the suture line meets the anterior margin.

DISCUSSION. P. obtusum has recently been revised by Whittington (1965) and Dean (1971) but a different interpretation to the latter author, regarding its morphology and its relationship to Pharostoma leptaenarum (Törnquist, 1884), is presented here. As with other Pharostoma taxa, uncertainties have arisen due to a lack of well preserved topotype material. In order to elucidate these problems it is necessary to recall the history of both species.

Warburg (1925, p. 423) considered P. leptaenarum to be a junior synonym of P. obtusum. Whittington (1965, p. 56) said Warburg's earlier description (1925, p. 155) of P. leptaenarum was applicable to McCoy's holotype, the only topotype specimen he had available, except for the fringe of spines on the anterior border of the Swedish species; but he noted Warburg's remark that the spines are not readily seen unless the anterior cranidial margin is well preserved, and in McCoy's holotype it is not. Whittington continued to separate P. leptaenarum from P. obtusum pending better material from the Chair of Kildare.

In collecting for his monograph on the Chair of Kildare trilobite fauna Dean found only a few incomplete cranidia and pygidia of P. obtusum despite a considerable effort to obtain more. He placed P. leptaenarum in the synonymy of P. obtusum, believing that neither species had a "fringe of forwardly directed spines". Dean adopted this course of action because Warburg's illustrations and description of the spines in leptaenarum were based on material from Kallholn in the Siljan district, whereas Törnquist's holotype came from Doda. In evidence he figured (1971, pl. 18, fig. 11) well preserved cranidia from Doda which without doubt lack these spines.

As far as I am aware no-one has attempted to find Törnquist's holotype of P. leptaenarum though it has now been traced in the Palaeontological Institute, University of Lund (IPLU LO593t). Its present condition is identical in all respects to Törnquist's figure (1884, pl. 1, fig. 44) except that the occipital ring is now missing, but this could easily have been broken off subsequent to Törnquist's work. The delicate anterior border is not as well preserved as one would have liked, and has been somewhat abraded during a previous preparation though it does not seem to have any protruding spines.

My examination of material from Kallholn has confirmed Warburg's description of cranidia from this locality, as a fringe of spines can be clearly observed on each specimen, and this feature would therefore appear to provide the basis for the erection of a new species. However I am at variance with Dean's interpretation of the anterior border of his Irish cranidia, and believe the Kallholn material to be conspecific with P. obtusum.

In the event of a distinguishing character being poorly displayed by the holotype of a species, one is forced to rely more heavily on the evidence from topotype material. In the case of P. obtusum it is not possible to tell from the holotype the nature of the anterior border, but the Irish specimen illustrated by Dean (1971) on pl. 18, fig. 15 showed sufficient irregularity in the outline of its anterior margin to make one suspect the presence of short spines, and thus encourage its re-examination. This specimen (BM It1832) is refigured here (Pl. , fig.), and after comparison with the cranidia from Kallholn I am of the opinion that it has similar spines in the same positions on the anterior border. There is one sited exsagittally opposite the front of the palpebral lobe (on right side only), and another opposite the lateral margin of the frontal lobe; the medial spine is broken off but there is a scar here which doubtless testifies to its former existence at this point.

The internal mould specimens Whittington (1965, p. 57) referred to as _Pharostoma_ cf. _obtusum_ from the Rhiwlas Limestone (Rawtheyan) of N Wales were described as having the "bases of large tubercles (or short spines) scattered along" the "anterior border". Examples of this species (in the collections of the Nat. Mus. of Wales) have been examined, and I feel sure it is the same as _P. obtusum_. Accordingly I shall use the name _obtusum_ to include those specimens which show the characters outlined in the descriptions of Warburg and Whittington together with the spines on the anterior border. As none of the cranidia from Boda are known to exhibit anterior spines, I shall retain the name _leptaenarum_ for these specimens, admitting that they are otherwise identical to _P. obtusum_. The anterior fringe of spines may simply represent a difference of sex.

Only the species referred to as _Pharostoma_ sp. B. from the Upper _Chasmops_ Limestone of the Oslo region exhibits a comparable development of spines. Distortion of the Norwegian cranidium prevents a closer comparison though the tubercles ornamenting the glabella and fixed cheek seem coarser than those of _P. obtusum_.

OCCURRENCE. P. obtusum is confined to the Ashgill. Apart from the type locality, as here interpreted it is found in the Rawtheyan of the Bala district, N Wales, and in the Boda Limestone at Kallholn and Osmundsberg (Warburg 1925, pl. 4, fig. 5) in Dalarna, Sweden.

Pharostoma leptaenarum (Törnquist, 1884)

Plate 12, figs. 7, 8, 10, 12.

1884 Calymene Leptaenarum n.sp.; Törnquist, p. 41, pl. 1, fig. 44.

? 1906 Calymene pulchra BEYR.; Olin, p. 58, pl. 2, fig. 15.

1925 Pharostoma Leptaenarum Törnquist; Warburg (pars), p. 155, pl. 4, fig. 1, ? figs. 3, 4.

? 1936 Pharostoma rarum n.sp.; Cooper & Kindle, p. 369, pl. 53, fig. 5.

1960 Pharostoma leptaenarum (Törnquist); Whittard, p. 137.

? 1968 Prionocheilus rarus; Lesperance, pp. 148, 151.

1971 Prionocheilus obtusus (McCoy); Dean p. 42, pl. 18, fig. 11 only.

HOLOTYPE. Incomplete cranidium; IPLU L0593t; Pl. 12, figs. 7, 8, 12.

TYPE STRATUM AND TYPE LOCALITY. Boda (Upper Leptaena) Limestone, Boda, Siljan district of Dalarna, Sweden. The Boda Limestone is of Ashgill age.

ADDITIONAL MATERIAL. Five cranidia, IPLU 1938t IPLU unnumbered, BM It1829 (3 specimens).

DIAGNOSIS. As for P. obtusum except that it does not have a fringe of forwardly directed spines on the anterior border.

DESCRIPTION. The reader is referred to Warburg's (1925, p. 155) detailed description.

DISCUSSION. The holotype of P. leptaenarum is refigured for the first time since 1884. Dean (1971) illustrated topotype cranidia which closely match the type specimen. Characteristic of this species is the bluntly rounded frontal lobe, gentle fall of the moderately convex preglabellar field to the shorter, horizontally projecting anterior border, non-spinose anterior margin and the forwardly positioned eyes.

P. leptaenarum and P. obtusum are the last representatives of the genus and are inseparable but for the form of the anterior border (see diagnosis). P. rarum Cooper & Kindle, 1936 from the Ashgill of Quebec may be synonymous with leptaenarum, differences in the N American holotype, such as a shorter preglabellar field and larger cranidial tubercles, being accounted for by its juvenile condition (Dean 1971, p. 44). The Quebec species must be revised before a decision can be made. The cranidium of Pharostoma cf. rarum recorded by Ingham (1966, p. 486) from the Cautleyan of northern England has not yet been described.

Olin (1906, p. 58, pl. 2, fig. 15) referred a cranidium from his Trinucleus Beds (=Jerrestad Stage of Jaanusson 1963, p. 134, or approximately middle Ashgill) at Tosterup, Scania to "Calymene pulchra Beyrich". It has little in common with the Bohemian taxon yet points of resemblance to Ashgill species are numerous. Dean (1971, p. 42) considered it to be the same species as P. obtusum and P. leptaenarum. Although somewhat flattened, the specimen is well preserved and undoubtedly lacks any frontal spines which, according to the interpretation employed here, places it closer to the latter species. The crescentic area of the axial furrow beside lateral lobe 1p is far more dilated compared to that of the holotype of leptaenarum, though this need not be significant as specimens from Boda (Dean 1971, pl. 18, fig. 11) also differ from the holotype in this respect. In most characters the internal mould cranidium from the _Trinucleus_ Beds falls readily into the concept of _P. leptaenarum_ adopted herein yet a cast of the external mould reveals a relatively narrower preglabellar field - which is now almost equal in length to the anterior border. This is atypical of _leptaenarum_, results in one questioning its assignment to that species, and is reminiscent of _P. oelandicum_, _P. ornithoreos_, _P. rarum_ and _Pharostoma_ sp. A.

Of these species, _P. oelandicum_ can be easily discriminated from the Scanian cranidium by the more strongly arched outline to its frontal glabellar lobe and position of palpebral lobe which is sited opposite lateral glabellar lobe 2p.

P. ornithoreos has a longer preglabellar area and cuspidate outline to its anterior margin. _P. rarum_ and _Pharostoma_ sp. A (which may be conspecific) are both closely related to Olin's specimen, but seemingly distinguished by a more upturned anterior border and coarser cranidial tubercles. In the absence of additional material from Quebec, the Oslo Region and Scania, and without a revision of _P. rarum_, the range of variation of specimens from each area remains unknown. Thus whether they represent the same or more than one species is to a certain extent speculative. It is not possible for me to refer the Scanian specimen to either _P. rarum_ or _P. leptaenarum_ with certainty and their is scant justification for the erection of a new spatial (? or temporal) subspecies. For the present I have questionably placed it with _P. leptaenarum_. It is worthy of note that cranidia of _leptaenarum_ figured in this study and by Dean (1971), show a shallow but distinct depression running parallel with and confining the broad, low eye ridge on its posterior side. The _Trinucleus_ Shale cranidium clearly exhibits the same feature.

OCCURRENCE. Limited to the Boda Limestone at Boda. Possibly occurs in the Boda Limestone at Arfvet (Warburg 1925, pl. 4, fig. 3) and the _Trinucleus_ Beds at Tosterup, Scania.

Family GLAPHURIDAE Hupe, 1953

Genus THULINCOLA Tripp, 1962

TYPE SPECIES. Thulincola barbarus Tripp, 1962, p. 27, pl. 4, figs. 1a, b; from the Ordovician Barr Group, Valcourea confinis Flags (Llandeilo), Kirkdominae, Girvan District, Ayrshire. By monotypy.

DISCUSSION. The material on which Thulincola was established is very small and consists of poorly preserved internal moulds. Tripp referred his taxon to the Calymenidae and distinguished it from Pharostoma, the genus he considered to be its nearest relative. The taxonomic position of Thulincola is difficult to determine due to the nature of the type specimens, but it does not appear to be a calymenid.

Diagnostic of post - Arenig calymenids are the relatively well isolated (from each other) and independently convex (from the central glabellar area) lateral glabellar lobes. Pharostoma is unusual in that it often shows a distal shallowing of lateral furrow 1p, so that 1p and 2p lobes meet near the axial furrow. This is also the case in Thulincola, except in this genus the 1p furrow is abaxially weaker and in consequence the conjugation of lobes 1p and 2p is more strongly developed. A more striking difference in Thulincola is the 2p furrow which is reduced to a mere pit on the dorsolateral glabellar surface, does not reach the axial furrow, and results in the fusion of lobes 2p and 3p; this arrangement is unknown in all other genera assigned to the Calymenidae. In Pharostoma the 2p furrow is often slightly shallower abaxially but nevertheless distinctly separates the lateral glabellar lobes.

The apparently opisthoparian facial suture of Thulincola is uncommon in calymenids, but is not unknown (Pharostoma, Bathycheilus).

Unlike Pharostoma, Thulincola lacks a preglabellar field, though nearly all genera within the Calymenidae also have the preglabellar field absent.

The poorly preserved topotype hypostome, free cheek, pygidia and thoracic segments which Tripp (1962, pl. 4, figs. 5-9) referred to Thulincola are of calymenid type, but may not belong with the holotype cranidium. The isolated free cheek (Tripp 1962, pl. 4, fig. 5) shows both genal and lateral marginal spines, and this combination of characters is found elsewhere in the Calymenidae only in Pharostoma. The subrectangular glabellar outline of Thulincola is unknown in Pharostoma species of approximately Llanvirn to middle Caradoc age (P. nieszkowskii, P. simile) though later Ashgill taxa (P. obtusum) do show more subparallel axial furrows and bluntly rounded frontal lobe

In 1967 Tripp recorded Thulincola barbarus from the Upper Stincher Limestone of the Girvan district, and he figured (pl. 6, figs. 1, 2) two small internal moulds, one of which was a free cheek, and the other an incomplete individual. The free cheek shows a few marginal spines and, significantly, the remains of the visual surface of the eye which is composed of small lenses. The visual surface of the eye has not been previously observed in any member of the family and it is unlikely that this cheek belongs to a calymenid. The incomplete individual is ill-preserved, especially in the region of the glabella, and it is debatable as to whether it belongs to the same taxon as that from the Confinis Flags; its thoracic segments are calymenid-like.

Thus an examination of topotype material of Thulincola left much doubt regarding the assignment of this genus to the Calymenidae, largely because of its glabellar lobation and furrows. The preparation and restudy of two cranidia which Reed (1906, p. 138, unfigured) referred to as Calymene sp. ind. (a) and Calymene sp. ind.(b) from the stratigraphically later Balclatchie Conglomerate (lower Caradoc) of the Girvan district has helped resolve the problem. These specimens are somewhat distorted but retain their cuticle and must be regarded as congeneric, if not conspecific with T. barbarus. The more complete cranidium (BM In23399) shows clearly the adaxially convex, slit-like 1p furrow, pit-like 2p furrow and merged lateral glabellar lobes (see Pl. 13, fig. 1). These characters are sufficient to demand the removal of Thulincola from the Calymenidae.

Dr. R.A. Fortey (Brit. Mus. Nat. Hist.) kindly drew my attention to the similarity of the Scottish cranidia with members of the Glaphuridae Hupe, 1953. A comparison of Thulincola with species of Glaphurus Raymond, 1905, Glaphurina Ulrich, 1930 and Glaphurella Dean, 1971, which have been recently figured by Shaw (1968) and Dean (1971), suggests that Tripp's genus is not synonymous with any of these, though certain family likenesses are evident and it is possibly a glaphurid.

Fused lateral lobes and a glabella of moderate to strong relief (as in Thulincola) appear characteristic of all the genera in this family, while Glaphurus pustulatus (Walcott) has a pit-like anterior lateral glabellar furrow (see Shaw 1968, pl. 8, figs. 1, 2, 6), Glaphurina lacks a preglabellar field (Shaw, pl. 8, figs. 11, 13, 15) and in Glaphurella this feature is very narrow (Dean 1971, pl. 22, figs. 4, 7).

CALYMENID TRILOBITES FROM THE MIDDLE ORDOVICIAN OF THE OSLO REGION, NORWAY.

INTRODUCTION. This paper forms part of a series initiated by Professor Leif Størmer (1953) to investigate the stratigraphy, tectonics and palaeontology of the Norwegian Middle Ordovician. In common with the usage of previous authors (Henningsmoen 1960, Owens 1970), I have taken the limits of the Middle Ordovician in the Oslo Region to include strata from the base of the Upper Didymograptus Shale ($4a\alpha_1$) (= base of Didymograptus bifidus Zone) to the top of the Upper Chasmops Limestone ($4b\delta_2$). A detailed account of the stratigraphy and geographical districts of the area is given by Størmer (1953).

Hitherto there has been no formal treatment of any calymenid trilobite from the succession in question, and from the whole of the Norwegian Ordovician and Silurian only two species have been described (Størmer 1945, Whittington 1971). During the present study members of the family have been found to occur throughout the Middle Ordovician with the possible exception of the Upper Didymograptus Shale (see Table 1 and occurrence of Gravicalymene capitovata sp. nov.). They are most common and best preserved in the Upper Chasmops Limestone. Six of the eleven districts of the Oslo Region, in particular that of Oslo-Asker, have yielded calymenids of Middle Ordovician age.

TERMINOLOGY, TECHNIQUES AND MEASUREMENTS. These are the same as those outlined in the first part of this thesis.

BRITISH GRAPTOLITE ZONES	BRITISH SUCCESSION		MIDDLE ORDOVICIAN SUCCESSION OF OSLO - ASKER DISTRICT	CALYMENID TRILOBITES; STRATIGRAPHICAL DISTRIBUTION	DISTRICTS OF THE OSLO REGION: OSLO-ASKER	RINGERIKE	HADELAND	SKIEN-LANGESUND	EIKER-SANDSVÆR	NES-HAMAR
P. linearis	CARADOC	ONNIAN / ACTONIAN	Upper *Chasmops* Limestone 4b δ	*F.(Reacalymene) sp. nov.*			■			
D. clingani				*F. scabustula*	■					
				F. jemtlandica	■	■				
				P. narinosum	■					
				P. cf. foveolatum						■
				Pharostoma sp. A.	■					
		MARSHBROOKIAN	Upper *Chasmops* Shale 4b γ	*Flexicalymene sp. ind. 3*	■					
				Flexicalymene sp. ind. 2	■					
				Pharostoma sp. B	■					
		LONGVILLIAN UPPER		*P. cf. nieszkowskii*			■			
		LONGVILLIAN LOWER	Lower *Chasmops* Limestone 4b β	*F. cf. scabustula*	■					
C. wilsoni		SOUDLEYAN	Lower *Chasmops* Shale 4b α	*Flexicalymene sp. ind. 1*	■					
				F. cf. caractaci			■			
C. peltifer		HARNAGIAN		*Gravicalymene ? sp. indet*	■					
				G. aff. capitovata	■?				■?	
				P. cf. nieszkowskii	■					
?		COSTONIAN								
N. gracilis	LLANDEILO		*Ampyx* Limestone 4a β	*Q. lirella*	■			■		
G. teretiusculus			*Ogygiocaris* Shale 4a α_{3-4}	*Q. lirella*					■	
				G. capitovata					■	
D. murchisoni	LLANVIRN		Upper *Didymograptus* Shale 4a α_{1-2}	*G. capitovata*					■	
D. bifidus										

TABLE 1. Known stratigraphical and geographical distribution of calymenid trilobites, Middle Ordovician, Oslo Region. British graptolite zones and succession after Williams in Williams *et al.* 1972. Correlation of British Caradoc Stages with Norwegian succession after Dean 1960. Correlation of Llanvirn with Upper *Didymograptus* Shale after Henningsmoen and Spjeldnaes 1960.

SYSTEMATIC PALAEONTOLOGY

Family CALYMENIDAE Milne Edwards, 1840

Subfamily BATHYCHEILINAE Pribyl, 1953

Genus PHAROSTOMA Hawle & Corda, 1847

[= Prionocheilus Rouault, 1847; nomen oblitum]

TYPE SPECIES. Calymene pulchra Beyrich, 1846, pl.2, figs. 6a, b; from the Letna Formation (= lower Caradoc), Vesela, Bohemia. By monotypy.

DISCUSSION. Dean (1964) presented evidence to show that Prionocheilus Rouault, 1847 has priority over the universally employed Pharostoma Hawle & Corda, 1847 and he advocated the use of the senior synonym. Whittington (1965) made use of Article 23(b) of the International Code of Zoological Nomenclature and regarded Prionocheilus as a nomen oblitum, though Dean (1971) later stood by his original views. I am inclined to share the opinion of Whittington as the defence of the unchallenged junior synonym is the prime object of Article 23 (b) which is brought into effect to preserve stability of nomenclature.

I regard Beyrich as the author of the type species, Calymene pulchra (after Whittard 1960; against Vanek 1965).

Pharostoma cf. P. nieszkowskii (Schmidt, 1894)

Plate 1, figs. 1-5, 8, 9

MATERIAL. Seven incomplete cranidia, two of which have the cuticle partially remaining, PMO 91018, PMO 91021, PMO 91024-26, PMO 34161 (two specimens); two internal moulds of incomplete cranidia with attached thoracic segments, PMO 91020, PMO 91024;

one external mould of an incomplete cranidium, PMO 91031; one internal and one external mould of incomplete pygidia, PMO 91027, PMO 91030.

OCCURRENCE. All the specimens except three come from the Lower Chasmops Shale (4bα), NE side of Semsvannet, Oslo-Asker district. PMO 91021 is from the Lower Chasmops Shale (4bα), the tunnel at Billingstad, Oslo-Asker district. PMO 34161 is from the Cyclocrinus beds, Upper Chasmops Shale (4bγ), S of Røykenvik, Hadeland district.

DESCRIPTION. Glabella about as long as wide. Moderate inflation on the side of glabella between adaxial fork of lateral furrow 1p. Preglabellar field very gently convex (sag.). Anterior border appears steeply inclined. Anterior margin arched forwards. Eye ridge runs into axial furrow at about lateral furrow 3p. One small specimen (PMO 91020; Pl. 1, fig. 4) has both free cheek and rostral plate preserved as external moulds. Free cheek has a long genal spine. At the junction of lateral border and its doublure there are pit-like impressions which represent the counterpart of spines on the internal mould. Rostral plate ill-preserved but consists of border sector and what seems to be part of a doublure sector - as is normal for calymenids. The pits continue from the free cheek and are present at the junction of these two sectors.

Pygidium has six axial rings and six well marked pleural furrows. The most anterior pleural furrow almost reaches lateral margin, successively more posterior pleural furrows become gradually shorter.

DISCUSSION. This species represents the earliest member of Pharostoma from Norway. Öpik (1937, p. 22, pl. 15, fig. 4, pl. 16, text-figs. 1-3) described specimens of P. nieszkowskii from the Middle Ordovician Kukruse Stage (C_2) of Estonia, though Schmidt's syntypes from the same horizon await re-study. The Kukruse Stage is regarded by Williams (in Williams, Strachan, Bassett, Dean et al. 1972, p. 8) as coincident with the range of Nemagraptus gracilis (middle Llandeilo to upper Costonian). P. foveolatum (Törnquist, 1884) and P. narinosum sp. nov. are easily separated from P. nieszkowskii by their longer preglabellar field. Czechoslovakian species of Pharostoma all have a convex, roll-like anterior border in lateral profile, and Ashgill species such as P. obtusum (McCoy, 1846) a rather more subrectangular glabellar outline due to a bluntly rounded frontal lobe and less posteriorly diverging axial furrows. Characteristic of P. nieszkowskii is a moderately long preglabellar area and preglabellar field (respectively about one third to two fifths, and about one fifth as long as the glabella), a moderately inclined anterior border, and a medially pointed anterior cranidial margin.

The Norwegian material is not well preserved but the most complete, least distorted glabella (PMO 91025; Pl. 1, figs. 1, 2) is identical to that of a P. nieszkowskii specimen I have examined (RM Ar34406) from Kukruse, Estonia. Similarly, though the preglabellar area is complete on only one cranidium from Norway (PMO 91024; Pl. 1, fig. 3) it agrees in general with that of P. nieszkowskii except that the angular, pointed nature of the anterior margin is not so apparent. This may be accounted for by the fact that it is a slightly squashed internal mould; a similar discrepancy due to preservational differences has been observed in Estonian material (Öpik 1937, p. 22).

The Norwegian cranidium may also be compared with that of Pharostoma simile Thorslund, 1940 from the Lower Chasmops Limestone of Södermanland, Sweden. The cranidium of P. simile is indistinguishable from P. nieszkowskii except that it may attain a greater size (Thorslund 1940). Öpik (1937) described a non-topotype pygidium of P. nieszkowskii as having five axial rings, a terminal axial piece and six pleural ribs. Thorslund's specimens have eight to ten axial rings and seven to eight pleural ribs, and these characters formed the basis for his diagnosis of P. simile. The pygidium of the Norwegian material is more allied to P. nieszkowskii and I have therefore chosen to compare it with this species.

The anterior margin is missing on two Pharostoma cranidia from the Upper Chasmops Shale and they are here compared to nieszkowskii largely because of the likeness in glabellar morphology.

Outside Estonia P. nieszkowskii is present in the Middle Ordovician limestone with Lonchodomas rostratus (= "Ampyx" Limestone) from Tommarp, SE Scania, an horizon of approximately the same age as the Lower Chasmops Shale. These specimens were originally referred by Funkquist (1919, p. 36, pl. 1, figs. 5, 6) to Calymene pulchra (= Pharostoma pulchrum Beyrich, 1846).

Pharostoma cf. P. foveolatum (Törnquist, 1884)

Plate 1, figs. 6, 7

MATERIAL. Two small, incomplete cranidia, PMO 38555-56; coll. J. Kiaer, 1922.

OCCURRENCE. The beds above the coral limestone, Mjøsa Limestone (4b δ+), peninsular S of Bergvika, Helgøya, Nes-Hamar district.

DESCRIPTION. Lateral glabellar lobe 1p is longer (exs.) than wide, subrectangular in outline, separated from central glabellar lobe by a shallow furrow. Lateral furrow 1p extremely shallow at axial furrow, deepest around inner, anterior corner of lobe 1p. Lobe 2p isolated from central glabellar lobe by distinct furrow. Moderately deep furrow 2p runs inwards and backwards. Very small lobe 3p confined anteriorly by transversely directed furrow 3p. Dorsal surface of glabella rises well above height of lobes 2p and 3p, less so above lobe 1p. Frontal glabellar lobe arched forwards.

Preglabellar furrow deepest either side median line at two points about half the width of frontal lobe apart; shallowest at anterolateral margins of glabella where preglabellar field is somewhat swollen. Posterior part of preglabellar field is convex (sag. & exs.). Anterior border furrow shallow. Anterior border incomplete, but seems relatively long. Axial furrow expanded and crescent-shaped outside lobe 1p; shallowest outside lobe 2p. Anterior pit situated on outer side of axial furrow half-way along frontal lobe. Eye ridge runs into axial furrow between lobe 2p and anterior pit. Tubercles on glabella and anterior border much larger than on preglabellar field.

DISCUSSION. The total morphology of this species allies it to other Middle Ordovician Scandinavian taxa such as P. foveolatum, P. narinosum sp. nov. and P. simile. In particular the uncommonly long preglabellar area of the Helgøya species, estimated to be just less than half the length of the glabella in PMO 38556, is comparable only with P. foveolatum and P. narinosum.

P. narinosum is distinguished from P. foveolatum by the absence of a strongly convex (sag.) preglabellar field and a wider, more gently inclined anterior border. There is no doubt that large holaspid specimens of the new species show these marked differences. The Mjøsa Limestone species, however, shows a similarity in the structure of its preglabellar area to both P. foveolatum and P. narinosum. The more complete Mjøsa cranidium (PMO 38556) apparently has a fairly wide (sag.) anterior border, but it also shows the posterior part of the preglabellar field to be moderately convex. Difficulties arise in comparing these two small specimens with the very much larger material of P. foveolatum and P. narinosum, and from not knowing to what extent the form of their preglabellar area is a function of size.

It is possible that both cranidia develop a slightly concave (sag.) preglabellar field later in ontogeny and thus belong to P. narinosum. If this is so, the pattern of tubercles on the cranidium of narinosum also changes during growth. The two small Mjøsa cranidia both show substantially smaller tubercles on the preglabellar field than on the anterior border or glabella (as in P. simile Thorslund, 1940); the holotype of P. narinosum has tubercles of various sizes which are equally scattered over the whole cranidium. The ornamentation of P. foveolatum is not well known though one specimen I have seen (IPU Ar469) shows an increased concentration of tubercles on the glabella. In the absence of more complete material and a greater size range of specimens from Helgøya, the problem remains open. For the present, because the species has a sagittally convex preglabellar field, I have compared it to P. foveolatum (Törnquist, 1884).

Pharostoma narinosum sp. nov.

Plate 2, figs. 1-8

DERIVATION OF THE NAME. From the Latin, narinosus, broad-nosed, alluding to the expanded preglabellar area.

HOLOTYPE. An incomplete cranidium; PMO 81266; coll. N. Spjeldnaes, 1953; Pl. 2, figs. 1-4.

TYPE STRATUM AND TYPE LOCALITY. Upper Chasmops Limestone (4b δ), south side of north Raudholmen (= Raudskjaer), Oslo-Asker district.

ADDITIONAL MATERIAL. Two large incomplete cranidia, PMO 91448-49; coll. D.L. Bruton, D.J. Siveter, 1971.

DIAGNOSIS. Preglabellar area about half as long as glabella. Preglabellar field about one third as long as glabella and flat to weakly concave upwards in lateral profile. Anterior border projects gently forwards and upwards, is just greater than half as long as preglabellar field and slightly more than one third as long as preglabellar area.

DESCRIPTION. Subtriangular shaped glabella is about as wide as long and more convex transversely than along median line. Occipital ring is about 4.5 times as wide as long, almost flat (sag.), narrows towards axial furrow. Occipital furrow very narrow (sag. & exs.), sharply, though not deeply incised medially, becomes deeper abaxially. Lateral glabellar lobe 1p is subrectangular in outline and about one third as long and one third as wide as glabella. Lateral furrow 1p very shallow at axial furrow, increases in depth as it runs inwards and turns very sharply backwards around inner, anterior corner of lobe 1p. At adaxial end of furrow 1p, PMO 91448 (Pl. 2, figs. 5, 7) has a very gentle inflation on the side of the central area of glabella which is lacking in other specimens. Subtriangular lateral lobe 2p is connected at posterior abaxial corner to lobe 1p; it is more clearly separated than lobe 1p from, and is well below dorsal surface of, central area of glabella. Moderately deep lateral furrow 2p is directed inwards and backwards. Very small lobe 3p is longer (exs.) adaxially than abaxially because of short (tr.), shallow, transverse furrow 3p almost meeting furrow 2p at axial furrow. Outline of frontal glabellar lobe not evenly convex forwards but indented medially and just either side median line; in profile frontal lobe falls mildly to preglabellar furrow.

Preglabellar furrow generally shallow, but slightly more deep and best marked at indentations of frontal lobe. Preglabellar area about one third as long as cranidium. Preglabellar field about one third as long as glabella, is flat to gently concave upwards in lateral profile, and transversely it slopes down from median line to facial suture. A subcircular swelling occurs on posterior part of preglabellar field at each anterolateral margin of frontal glabellar lobe. Anterior border furrow weakly developed, especially abaxially. Anterior border has an almost flat dorsal surface which inclines forwards and moderately upwards; it narrows (exs.) near facial suture. In dorsal view anterior margin is moderately and evenly convex forwards.

Beside lateral glabellar lobe 1p, axial furrow expands into a flat-bottomed crescent-shaped area; around lobe 2p it shallows and is abaxially convex, it becomes more distinct again from here to a shallow anterior pit below side of frontal lobe. Between lobe 2p and anterior pit the extremity of an eye ridge abutts into axial furrow.

Posterior border is rather narrow (exs.) from axial furrow to fulcrum, thereafter expanding and swinging backwards towards facial suture (Pl. 2, figs. 6, 8). A rill-like, constantly narrow posterior border furrow fades at genal angle and is connected here to very weak lateral border furrow. Fixed cheek slopes more steeply and is more convex from palpebral lobe towards anterior border furrow than towards posterior border furrow. A shallow, broad depression runs diagonally outwards from near anterior pit to separate subcircular inflation on posterior part of preglabellar field from anterior part of fixed cheek; this depression fades out before reaching anterior border furrow. Trending forwards and inwards from palpebral lobe, mid-point of which is opposite anterior part of lobe 2p, is a broad, low eye ridge. Just behind and inwards from eye is an oval-shaped swelling which has its long axis directed slightly more forward than eye ridge. Posterior branch of facial suture runs transversely outwards from eye, then curves backwards towards posterior margin, more sharply backwards after crossing lateral border furrow. Anterior branch runs forwards and outwards to anterior margin.

The whole of the holotype cranidium, except all furrows but the anterior border furrow, is covered with fine pustules ranging up in size into moderately large tubercles. The larger tubercles often exhibit a conspicuous centrally positioned opening. Two faint, narrow (exs.) ridge-like structures run diagonally outwards on the anterior part of the fixed cheek.

DISCUSSION. P. narinosum sp. nov. is most closely related to P. foveolatum (Törnquist, 1884) from the Middle Ordovician Kullsberg Limestone of Dalarna, Sweden. Both species have provided large cranidia with an unusually long preglabellar field and preglabellar area. They are also very alike in glabellar morphology, irregularity in outline of the frontal glabellar lobe, position of the eye, and the subcircular and oval swellings on the preglabellar field and fixed cheek respectively. _P. foveolatum_ is distinguished by its moderate to strongly convex upwards (sag. & exs.) preglabellar field and a shorter, more steeply upturned anterior border. The anterior border is only about one fifth to one quarter as long as the preglabellar area in the Swedish species, compared to more than one third in the Norwegian.

There is some evidence to suggest that the preglabellar field and (therefore) preglabellar area of _P. foveolatum_ become relatively longer during the holaspid period (Warburg, 1925, p. 164). There is not enough size-range in the limited Norwegian material to deduce whether a similar increase takes place.

Pharostoma simile Thorslund, 1940, another related species, differs from _P. narinosum_ through its sagittally shorter, convex preglabellar field, shorter preglabellar area, more upturned anterior border, more angular outline to the anterior margin, and the contrast in size between the rather fine tubercles ornamenting its preglabellar field compared with the larger ones on its anterior border and glabella.

As with _P. narinosum_, _P. simile_ displays a number of faint, subparallel ridges which run diagonally forward and outward across the anterior part of the fixed cheek towards the junction of the anterior margin and facial suture. Though on a much smaller scale, this type of cuticular sculpture resembles that described by Öpik (1961, pp. 410-38) in Cambrian redlichiids and ollenelids and regarded by that author as an external expression of internal caeca.

P. narinosum, *P. foveolatum*, *P. simile* and *P. nieszkowskii* form a closely-knit group in the Middle Ordovician of Baltoscandia. *P. narinosum*, like other sympatric *Pharostoma* species, is scarcely represented in the Oslo Region.

OCCURRENCE. The two additional specimens (PMO 91448-49) both come from the Upper *Chasmops* Limestone (4b δ), one metre below the Lower *Tretaspis* Shale (4c α), Kalvøya, Baerum, Oslo-Asker district.

Pharostoma sp. A

Plate 3, figs. 1, 4-7

MATERIAL. Two small, incomplete cranidia, both present on the same block, PMO 81312; coll. Nikolaisen, Bruton, Hamar, 1967.

OCCURRENCE. 1.7m below the top of the Upper *Chasmops* Limestone (4b δ), N Raudsjaer, Oslo-Asker district.

DESCRIPTION. Cranidium twice as wide as long (sag.). Glabella slightly longer than wide. Lateral lobe 1p is subtriangular in outline, about twice as long as lobe 2p, separated from median lobe of glabella by faint longitudinal depression. Lateral furrow 1p is shallow at axial furrow, becomes deeper as it curves inwards and backwards, finally turning more inwards towards median line. A short anterior branch from furrow 1p runs forwards to meet lateral glabellar furrow 2p, thus isolating lobe 2p. Lateral lobe 3p extremely small. Lateral furrow 3p very weakly developed. Frontal lobe is only gently convex forwards in outline; slopes quite steeply to shallow preglabellar furrow.

Preglabellar area and preglabellar field very short, only about one fifth and less than one tenth as long as the glabella respectively. Preglabellar field becomes more convex (exs.) and wider abaxially where fixed cheek is extended forwards and inwards. Anterior border furrow shallow. Anterior border marginally wider than preglabellar field, is inclined forwards and upwards. Anterior margin of the more complete specimen is somewhat pointed forwards medially; there is also a suggestion, on both specimens, that anterior border is a little more inflated opposite (exs.) the innermost part of furrow 2p.

Axial furrow is flat-bottomed, widest and crescent-shaped beside lobe 1p, much narrower beside lobe 2p, slightly constricted (tr.) by the eye ridge opposite lobe and furrow 3p.

Posterior border is strongly convex at axial furrow, less so near facial suture. Posterior border furrow is exsagittally narrow and deep. Part of the lateral border and border furrow are distinctly present on the posterior part of fixed cheek. Palpebral lobe mid-point is opposite anterior margin of lobe 2p. Broad (exs.), low eye ridge is directed towards lobe 3p. Anterior branch of facial suture runs forwards and slightly inwards to anterior margin. Posterior branch curves broadly outwards and increasingly more backwards to posterior margin. Rounded tubercles of medium to large size cover most of the cranidium excluding furrows and preglabellar field. Smaller tubercles are more infrequently scattered.

DISCUSSION. Material of this taxon is well preserved, though is incomplete and there are only two cranidia available. With the exception of Pharostoma sp. B, it differs from all other species in the Norwegian succession in having a very short preglabellar field and preglabellar area, and rather coarse cranidial tubercles. The preglabellar field is as short as in any other species (apart from, perhaps, P. matutinum (Dean, 1966) from the Arenig of SW France), and can best be compared with that of P. oelandicum Angelin, 1854 from the Macrourus Limestone erratics of Öland, or P. rarum Cooper & Kindle, 1936 from the Ashgill of Quebec. The shape of the glabella and outline of frontal glabellar lobe of Pharostoma sp. A show affinities with later Ashgill taxa rather than with earlier Middle Ordovician ones. For example P. nieszkowskii, P. simile, P. foveolatum and P. narinosum all have a frontal glabellar lobe that is more arched forwards medially in comparison with that of Pharostoma sp. A or P. rarum.

P. oelandicum is similarly distinguished from Pharostoma sp. A by the outline of its frontal lobe, together with more posteriorly positioned eyes, a horizontally projecting anterior border and less coarse cranidial tubercles.

P. obtusum (McCoy, 1846) and P. leptaenarum (Törnquist, 1884), both Ashgill taxa, have a longer preglabellar field (about one fifth to one seventh as long as the glabella), a horizontally protruding anterior border and finer surface tubercles on the cranidium.

The specimen referred by Olin (1906, p. 58, pl. 2, fig. 15) to 'Calymene' pulchra Beyrich from the Trinucleus Beds at Tosterup, Scania is completely unlike the Bohemian species and best allied to P. leptaenarum and Pharostoma sp. A. A stronger relationship with P. leptaenarum is likely because of its flat lying anterior border and small exoskeletal tubercles.

As far as can be determined the incomplete and distorted cranidium of Pharostoma sp. B conforms well with Pharostoma sp. A, but the anterior border of the former displays a fringe of short, forwardly-directed spines which are apparently absent in the Chasmops Limestone specimens. It may be noted, however, despite the imperfect preservation of the anterior border in Pharostoma sp. A, it is seen to be somewhat pointed at the median line (see description).

P. rarum needs to be redescribed with the aid of larger topotype cranidia as its holotype is a juvenile cranidium and was the only specimen known when the species was erected (Dean 1971, p. 42). Dean noted that the preglabellar field of P. rarum Cooper & Kindle, 1936 seems shorter and the glabellar tubercles larger than in P. obtusum (McCoy, 1846), though he considered these features possibly a result of the immature nature of the holotype, and questionably placed rarum in the synonymy of McCoy's taxon. Bearing this immaturity in mind, evidence from the original description and illustration of P. rarum (Cooper & Kindle 1936, p. 369, pl. 53, fig. 5) suggests it may be closer to Pharostoma sp. A than any other named species. The two characters given by Dean which possibly differentiate rarum from obtusum were listed above, together with a more upturned anterior border, as those discriminating Pharostoma sp. A from P. obtusum.

Extra material of Pharostoma sp. A, Pharostoma sp. B and P. rarum are required to make known their range of variation. Pharostoma sp. A may be synonymous with Pharostoma sp. B, or with Pharostoma rarum or neither. With the limited amount of material available I am uncertain as to the identification of the Upper Chasmops Limestone cranidia at the specific level and have used nomenclatura aperta for this species.

Pharostoma sp. B

Plate 3, figs. 2, 3.

MATERIAL. Distorted and incomplete external moulds of two cranidia, PMO 81535, PMO 81551; one internal mould of a distorted, incomplete cranidium and its counterpart, PMO 81538, PMO 81548; coll. N.Spjeldnaes, 1957.

OCCURRENCE. Upper Chasmops Shale (4b γ), Hvalstad skjaeringen, Oslo-Asker district.

DESCRIPTION. Although the material of this species is squashed, it appears to have a very narrow (sag.) preglabellar field (PMO 81538). Short, obtusely pointed spines project from the anterior margin. One spine is at the median line, with a smaller one either side at about one third the width of the frontal lobe apart, and one either side these opposite (exs.) the side of the frontal lobe. A probable fourth spine (counting abaxially from the median line) lies opposite (exs.) the front of the palpebral lobe. Axial furrow is typical of Pharostoma, expanded (tr.) outside lateral lobe 1p. Broad (exs.) eye ridge is present. Fixed cheek has a convex (exs.) posterior border and narrow, deep border furrow; both posterior border and border furrow join the posterior parts of lateral border and border furrow which then run forward to the facial suture.

Ornament on the cranidium is the same as for Pharostoma sp. A. - dominated by rather coarse tubercles.

DISCUSSION. The few cranidia at hand are incomplete and distorted - for instance the palpebral lobes are more posteriorly situated than would be normal - yet sufficient characters remain to associate this species with Pharostoma sp. A (see previous discussion). In common with Pharostoma sp. D, P. obtusum (McCoy, 1846) from the Chair of Kildare Limestone, Eire, also has a fringe of spines on its anterior border. The two taxa seem fairly closely related but the Irish species exhibits less coarse tubercles on the cranidium.

Subfamily FLEXICALYMENINAE subfam. nov.

TYPE GENUS. Flexicalymene Shirley, 1936.

DIAGNOSIS. Glabella has three to four lateral lobes and furrows which are, respectively, well inflated and distinct. Glabellar outline varies from parabolic to bell-shaped. Facial sutures gonatoparian (exceptionally proparian in some species of Flexicalymene). No preglabellar field. Lacks buttress from fixed check to lateral glabellar lobes. No ala or crescentic area outside lateral lobe 1p. Hypostome lacks protuberance on anterior lobe. Genal spines absent .

DISCUSSION. The importance given (Shirley 1936, p. 392; Whittington 1971) to the presence or absence of the papillate-buttress structure on the cranidium in calymenid phylogeny has been sustained by the present study. But hitherto there has only been informal grouping of buttressed and non-buttressed calymenid genera, and most authors have followed the 'Treatise' classification in combining all these genera, apart from Pharostoma, in the subfamily Calymeninae. The buttressed genera and many of the non-buttressed genera placed in this subfamily are here regarded as two evolutionary stocks (Shirley 1936). Accordingly the new subfamily Flexicalymeninae is erected herein to accomodate most of the non-buttressed forms, including (besides the type genus) Gravicalymene Shirley 1936, Thelecalymene Whittington, 1971, Platycalymene Shirley, 1936 and Palacalymene gen. nov. (see Chapter F). Work has been undertaken on a revision of various species in this subfamily (for example F. dilatata (Tullberg, 1882), F. declinata (Hawle & Corda 1847), F. incerta Barrande, 1846), and in a separate paper a full discussion of the Flexicalymeninae will be given.

Genus FLEXICALYMENE Shirley, 1936

[= Onnicalymene Dean, 1962]

TYPE SPECIES. Calymene Blumenbachii var. caractaci Salter, 1865, p. 96, pl. 9, fig. 3; from the Marshbrookian Stage (Caradoc), Zone of Dalmanella wattsi, Acton Scott Lodge, near Acton Scott, Shropshire. By original designation of Shirley 1936, p. 395.

DISCUSSION. In 1962 Dean diagnosed his new genus Onnicalymene as "Generally similar to Flexicalymene, but distinguished by anterior border, which is short and steeply inclined forwards, and by position of palpebral lobes, opposite third glabellar furrows and frontal portion of third glabellar lobes. Thorax with thirteen segments". At the same time he attributed four species to his new taxon - F. jemtlandica Thorslund, 1940, F. laticeps Bancroft, 1949, F. salteri Bancroft, 1949, and F. onniensis Shirley, 1936; the latter was selected as the type species. The genus was recorded by Dean as occurring in strata of Onnian to Pusgillian age, and found in England, Wales, Sweden, and S Norway.

Contrary to Dean's claim, it appears to me that the anterior border in each of the above species is not significantly different to that found in taxa generally accepted as belonging to Flexicalymene. In terms of length, F. onniensis has a shorter anterior border than

F. caractaci, but the length of the anterior border in such species as F. incerta (Barrande, 1846) and F. acantha Bancroft, 1949 is also comparable with that of onniensis. As regards the inclination of the border, the range of variation between, say, that of F. cambrensis (Salter, 1865) and F. caractaci is wide enough to encompass the variation shown by the species Dean referred to Onnicalymene. Thus separation of Onnicalymene from Flexicalymene depends solely on one character, the position of the palpebral lobe. Species of Flexicalymene typically have the palpebral lobe centred opposite lateral glabellar lobe 2p; those assigned to Onnicalymene, according to Dean, have it relatively farther back.

An examination of the type species of Flexicalymene and Onnicalymene reveals that F. caractaci has the palpebral lobe centred opposite lateral lobe 2p whereas F. onniensis has it centred opposite the outer part of furrow 1p. It should be noted, however, that in F. onniensis the palpebral lobe is rarely preserved and normally its position is determined from internal mould specimens. In the Upper Chasmops Limestone of the Oslo Region the many superbly preserved specimens of F. jemtlandica and F. scabustula sp. nov., both of which belong to the onniensis group of species, allow an accurate assessment to be made of the palpebral lobe position. Amongst specimens which must be regarded as conspecific, continuous variation is observed in the position of the palpebral lobe mid-point from opposite the posterior part of lobe 2p to the outer part of furrow 1p. In the case of F. jemtlandica compare PMO 91079 (Pl. 4 fig. 1) with PMO 81308 (Pl. 3 fig. 10) and PMO 81112/9/2 (Pl. 4 fig. 9); in the case of F. scabustula sp. nov. compare PMO 81138 (Pl. 6 fig. 8) with PMO 81250 (Pl. 6 fig. 1) and PMO 5491 (Pl. 6 fig. 9). Therefore the main character by which Onnicalymene was distinguished from Flexicalymene is seen to be gradational between the two genera and I am forced to regard them as synonymous. The tendency by the taxa referred to Onnicalymene to have a more posteriorly situated eye lobe is indiscrete, and worthy of recognition only by use of the informal species group category.

Flexicalymene cf. F. caractaci (Salter, 1865)
Plate 8, figs. 5, 7

MATERIAL. One cranidium, PMO 8173; coll. J. Kiaer, 1923.

OCCURRENCE. Lower Chasmops Shale (4bα), small quarry south of 143 Ringsaas, Ringerike district.

DESCRIPTION. Glabella is longer than wide, its outline is subtriangular. The three lateral glabellar lobes are graduated in size. Lobe 1p is subquadrangular, lobe 2p is subcircular. On side of central glabellar area between lobes 1p and 2p there is a small intermediate lobe. Frontal lobe has sub-parabolic outline, slopes steeply to preglabellar furrow, and reaches as far as the most anterior part of the fixed cheek. Preglabellar furrow shallow and wide (sag.). Long anterior border is moderately upturned. Palpebral lobe centred opposite lateral lobe 2p.

DISCUSSION. The lectotype of F. caractaci comes from the Marshbrookian of Shropshire. Shirley (1931, p. 25) was the first to revise the taxon, and it has since been commented on by Dean (1962, p. 114; 1963, p. 217) and Whittington (1965, p. 26). The Norwegian cranidium described here agrees in many respects and is best compared with F. caractaci though its anterior margin appears somewhat less evenly rounded than that of typical Shropshire specimens.

In this feature it is not unlike F. declinata (Hawle & Corda, 1847) from Czechoslovakia, but the Bohemian species has more anteriorly posititioned palpebral lobes and occurs considerably later in the Ordovician (Ashgill).

Based on Dean's (1960) correlation with the British succession, the Ringerike specimen is stratigraphically earlier (Harnagian or Soudleyan) than Welsh Borderland material of F. caractaci, yet it is undoubtedly closer to caractaci than to taxa of approximately the same age from Britain (Flexicalymene (Reacalymene) limba; Flexicalymene acantha). But calymenids which have been compared with F. caractaci have been recorded in strata of Longvillian age from Shropshire (Dean 1963, p. 218), Cross fell (Dean 1962, p. 114) and N Wales (Whittington 1965, p. 62), so that specimens of the caractaci type were also in existence in Britain before Marshbrookian times. This is substantiated by the presence of F. cobboldi Dean, 1963 in the Longvillian of Shropshire, a species regarded by Dean as close to caractaci but differing by its shorter glabella, yet considered by the present author to fall within the range of variation of F. caractaci.

Flexicalymene jemtlandica Thorslund, 1940

Plate 3, figs. 8-11; Plate 4, figs. 1-9, Plate 5, figs. 1-9, 11

1940 Flexicalymene jemtlandica n. sp.; Thorslund, p 147, pl 12, figs. 19, 20, non figs. 21, 22.

1949 F. jemtlandica Thorslund; Bancroft, p. 306.

1960 F. jemtlandica Thorslund; Dean, p. 86.

1962 Onnicalymene jemtlandica (Thorslund); Dean, p. 113.

? 1968 F. caractaci; Whittington, p. 115 (specimens not seen)

HOLOTYPE. Poorly preserved cranidium; SGU unnumbered; coll. P. Thorslund, 1936; figured Thorslund 1940, pl. 12, figs. 19, 20.

TYPE STRATUM AND TYPE LOCALITY. Ordovician, Zone of Dicranograptus clingani, overthrust beds, a cutting 0.4 km west of Skute, Stengärde, Jämtland, Sweden.

ADDITIONAL MATERIAL. More than thirty five cranidia and pygidia, several (more than five) free cheeks, hypostomes and rostral plates, all of which are housed in the Palaeontologisk Museum, Oslo.

DIAGNOSIS. Frontal glabellar lobe is about level with the fixed cheek. Lateral glabellar lobe 2p often considerably smaller than lobe 1p. In profile glabella falls evenly from occipital furrow to shallow preglabellar furrow. Anterior border not strongly inclined. Anterior branch of facial suture abaxially convex, runs forwards and inwards. Rounded projections on glabella are of two types: fine, closely spaced granules and medium sized, widely spaced tubercles.

DESCRIPTION. Cranidium is about twice as wide as long. Glabella is longer than it is wide, subparabolic in outline - its sides being rather straight as axial furrows run forward and inward from middle of lobe 1p, in lateral view it falls in an even smooth curve from furrow 1p to anterior face of frontal lobe, then marginally more steeply to preglabellar furrow. Occipital ring is about four and a half to five times as wide as long, narrows gradually behind lobe 1p to axial furrow where it is slightly inflated but without any discrete node; in lateral profile it is almost flat, stands just above dorsal surface of median glabellar lobe. Between basal glabellar lobes occipital furrow runs transversely, behind them it swings more posteriorly; in cross-section it is deeply incised and V - shaped with the posterior slope being shorter and more steeply inclined than the anterior. Lateral lobe 1p is large, subrectangular in outline, not quite one third as wide as the glabella. A deep glabellar furrow 1p runs inwards and backwards from axial furrow, turns more sharply posteriorly on reaching frontomedian lobe, is continued over adaxial neck of lobe 1p as a broad, shallow depression to meet occipital furrow; short anterior branch of furrow 1p crosses inner neck of lobe 2p; there is no intermediate lobe between anterior and posterior branches. Moderately inflated lobe 2p is highest adaxially and slopes steeply downwards and outwards to axial furrow (Pl. 4, fig. 2). Lobe 2p is generally less than half the length of 1p, but often there is a considerably greater size difference between these two lobes. Transversely directed furrow 2p turns backwards at central glabellar area around lobe 2p. Lobe 3p is about half as big as 2p and of the same basic form, perhaps a little more elongate (tr.). Sharply incised lateral furrow 3p barely reaches the base of the axial furrow. A faint furrow 4p may be present ascending from the posterior part of anterior pit. Frontal glabellar lobe is slightly greater than half as wide as glabella across lobes 1p, has a rather blunt anterior margin with rounded anterolateral corners and does not overhang preglabellar furrow or project beyond fixed cheeks.

Next to lobe 1p axial furrow is deepest and has vertical abaxial side, it becomes shallower at lobes 2p and 3p, finally merges anteriorly into preglabellar furrow. Anterior pit situated in axial furrow half-way along the side of the frontal lobe. In lateral view very shallow preglabellar furrow passes smoothly into weakly upturned anterior border which then turns sharply over, its outer side descending but a short distance before meeting rostral suture (Pl. 6, figs. 2, 6). Anterior margin of cranidium is feebly convex forwards in dorsal view; in frontal view it is gently arched.

Posterior border of cranidium is narrow and tightly convex (exs.) from axial furrow to fulcrum, expands rapidly in width distally from fulcrum to a point near genal angle, thereafter narrowing slightly to facial suture. Posterior border furrow has steeper and narrower posterior than anterior slope and just adaxially from facial suture swings backwards in an arc-like fashion (Pl. 3, fig. 9; Pl. 4, fig. 8). From palpebral lobe fixed cheek slopes gently to posterior border furrow; in front of palpebral lobe fixed cheek is noticeably steeper and more convex. Mid-point of moderate to strongly sloping (tr.) palpebral lobe varies from opposite posterior half of lobe 2p (PMO 91079, Pl. 4, fig. 1) to opposite outer part of furrow 1p (PMO 81112/9/2, Pl. 4, fig. 9). Very faint trace of eye ridge is seen on some specimens running from anterior part of palpebral lobe towards lateral furrow 3p (PMO 81308, Pl. 3, figs. 9, 10).

Posterior branch of facial suture is directed transversely to a point opposite (exs.) mid-way between fulcrum and genal angle, then bends more backwards to lateral border, then runs exsagittally for a short distance and finally trends outwards to bisect posterior and lateral margins. Anterior branch of suture proceeds forwards and inwards in a broad, abaxially convex curve to cross anterior margin, thereafter cutting across the very narrow outer side of the anterior border and almost immediately meeting the rostral suture. Lateral border furrow on free cheek is extremely shallow, especially posteriorly.

Rostral suture runs very close to and is parallel with the anterior cranidial margin. Connective suture is very faintly convex, runs strongly inwards, forms acute angle with rostral suture. Border sector of rostralplate is widest medially, shaped like a boomerang. Anterior border of hypostome is reflexed ventrally; anterior border furrow represented only by a broad depression between anterior border and median body. Moderately large anterior wing has distinct, dorsally directed pit. Lateral border is convex (tr.); lateral border shallowest at mid-length. Posterior margin is bifid due to expansion of border into two sharply-pointed spines. Between these spines, posterior border is much narrower (sag.) and the border furrow short (tr.) though distinctly impressed. Anterior lobe of median body is more inflated (sag. & tr.) and greater than twice the length of crescent-shaped posterior lobe. A faint, U-shaped median furrow connects two smooth, non-inflated, oval maculae then continues forwards to lateral border furrow.

Isolated thoracic segments show no unusual characters. Pygidium is slightly more than twice as wide as long. Axis is less than one third as wide as pygidium but relatively wider on smaller specimens (compare PMO 5575, Pl. 5, fig. 5 with PMO 81109, Pl 5, fig. 4), has five or six axial rings each of which is widest (sag.) medially, and a terminal axial piece. Ring furrows best marked distally, furrows one to four are complete, furrows five and six are indistinct and often discontinuous. Axial furrow not deep. Pleural region has five pleural and five interpleural furrows. Pleural furrows are fractionally shorter than interpleurals, at least the first three are more distinct proximally than distally, and the first one runs onto smooth pleural facet. Interpleural furrows are strongest distally, faintest at one third their length from axial furrow; fifth interpleural furrow forms side of postaxial sector and sometimes merges with fifth pleural furrow. Anterior pleural band of each pleura is much narrower than posterior pleural band but this distinction becomes progressively less marked from first to fifth pleura and within each pleura from axial furrow to lateral margin. (For variation in pygidium see discussion).

Ornament of the cranidium, particularly the glabella, consists of two main sizes of rounded projection. Widely spaced, medium sized tubercles are liberally scattered on glabella and anterior margin, some of which are perforate; the size and number of these tubercles decreases on inner part of fixed cheek and they are almost absent on outer part of fixed cheek. Secondly, there is a very fine, densely granulate surface to the whole cranidium (Pl. 5, fig. 11). Free cheek is covered with fine granules and an occasional low tubercle except for its lateral border which has closely spaced oval shaped tubercles anteriorly with more circular ones towards genal angle. Hypostome covered with fine tubercles and granules (particularly on lateral and posterior borders) except for smooth maculae. Ornament on axis and most of pleural region of pygidium is similar to that on glabella except larger tubercles are closer together. Inner part of pleural region shows marked decrease in numbers of tubercles, but still has granulation. Tubercles are lacking in deepest parts of furrows.

DISCUSSION. This species was founded by Thorslund on comparatively poorly preserved material from Jämtland. It is the characteristic calymenid of the Upper Chasmops Limestone (4b δ), the most abundant member of the family from the Oslo Region, and the excellently preserved specimens provide much new morphological information on the taxon. The Norwegian cranidia agree well with the holotype (which has been examined and will be figured elsewhere) except the anterior border in the former is usually a little less upturned.

Variation in the position of the palpebral lobe has been dealt with in the generic discussion. The palpebral lobes on the holotype are only partially complete but appear to be centred opposite the posterior half of lateral lobe 2p. Some of the Norwegian specimens display a rather shorter pre-glabellar area than is typical (compare Pl. 4, fig. 7 with Pl. 4, fig. 9), but as they conform with the more normal type of cranidium in other features I have regarded them all as conspecific.

A series of pygidia (PMO 5575, PMO 81313, PMO 81109 - pl. 5, figs. 5, 1, 3-4 respectively) from 3.8 mm to 11.5 mm wide (tr.) exhibit changes in morphology during growth. Compared with the two larger specimens, in the smallest pygidium (PMO 5575) the pleural and interpleural furrows are more equally impressed, the axis is wider (anteriorly) relative to the width of the pygidium, more axial rings are visible (six as opposed to five), the surface tubercles are coarser, and the axial furrow is more distinct behind the terminal axial piece.

The hypostome of <u>jemtlandica</u> is representative of the genus and does not have a projection on the anterior lobe. The basic construction of the rostral plate into a border and doublure sector typifies that for the family as a whole, though in comparison with the few previously described rostral plates of <u>Flexicalymene</u>, for example that of <u>F. senaria</u> (Conrad, 1841; see Evitt and Whittington 1953, p. 49 pl. 9, fig. 3), the rostral suture is more medially vaulted, less evenly arcuate.

From an examination of the holotype and other specimens, <u>F. onniensis</u> from the Onnian of Shropshire, Wales and northern England is easily separated from <u>jemtlandica</u> in the following respects. In side profile the dorsal surface of the glabella maintains a more horizontal attitude from the occipital furrow before beginning a slightly steeper descent to the preglabellar furrow; the occipital furrow is not so incised behind the central area of the glabella; the 2p lateral lobe is much larger relative to 1p lobe - this has the effect of making the glabellar outline appreciably more parabolic; there is often a small intermediate lobe between the fork of furrow 1p; the frontal lobe usually projects beyond the fixed cheek; and while the tubercles ornamenting the glabella are of a similar size to those of jemtlandica, there is no clear division into finer granules and medium-sized tubercles, and the latter appear to be closer together. In addition the preglabellar area of onniensis is generally shorter, and the upper, dorsal surface of the anterior border a little more puffy. The specimens assigned to jemtlandica with the shorter preglabellar area are reminiscent of onniensis in this character.

F. salteri from the Actonian of Shropshire is the nearest species to jemtlandica. The length of the glabella to fixed cheek, depth and form of the preglabellar furrow, outline of anterior margin, course of facial suture, nature of fixed cheek, and especially the type of preglabellar area are alike in the two taxa. Moreover although the sub-triangular outline to the glabella is quite diagnostic of F. salteri, it is more closely approached by some specimens of F. jemtlandica than any other species. F. salteri differs further through its relatively larger lateral glabellar lobe 2p, rounded frontal lobe, substantially wider (sag.) occipital ring and tightly set glabellar tubercles. The palpebral lobe is similarly situated in both species, if anything salteri has it a shade farther back and it has not been seen to vary so much in position as that of jemtlandica. The holotype of salteri is an internal mould and for purposes of comparison with the excellently preserved Scandinavian material the paratype (BM In42099) and another specimen (BM In59736) have largely been used.

OCCURRENCE. This species has been recorded from the Upper Chasmops Limestone (4b δ) at Raudskjaer (very common), Baerum, Asker and Terneholmen in the Oslo-Asker district, and Ringsaas and Norderhov in the Ringerike district. It is also present in the Lower Tretaspis Shale (4c α) at Nakholmen, Oslofiord (PMO 8930) and the Tretaspis Limestone (4c β) at Ringsasen, Ringerike (PMO 58745).

Apart from the type locality, Thorslund (1940) figured Swedish material from the Upper Chasmops Limestone (autochthonous beds) at Slandrom, Jämtland. This is here distinguished from F. jemtlandica (see discussion of F. scabustula sp. nov.).

Flexicalymene scabustula sp. nov.

Plate 5, fig. 10; Plate 6, figs. 1-9; Plate 7, figs. 1-15

? 1940 Flexicalymene jemtlandica n. sp.; Thorslund (pars) p. 147, pl. 12, figs. 21, 22, non figs. 19, 20.

DERIVATION OF THE NAME. From the latin, scabra, rough, and crustula, diminutive of crusta, shell, referring to the relatively large, coarse glabellar tubercles.

HOLOTYPE. Well preserved cranidium; PMO 81250; coll. G. Henningsmoen 29. 9. 62; Pl. 6, figs. 1-4.

TYPE STRATUM AND TYPE LOCALITY. Upper thick limestone bed, Upper Chasmops Limestone (4b δ), N Nakholmen, Inner Oslofiord, Oslo-Asker district.

ADDITIONAL MATERIAL At least fifteen incomplete cranidia, three free cheeks, three hypostomes, one rostral plate, four pygidia, plus a few isolated thoracic segments and numerous other fragments.

DIAGNOSIS. In profile the glabella is horizontal until lobe 2p, thereafter falling moderately steeply to preglabellar furrow. Anterior border somewhat convex (sag.). Anterior branch of facial suture more or less straight, runs forwards and inwards. Surface of glabella dominated by large, rough tubercles.

DESCRIPTION. Glabella is as long as fixed cheek and longer than it is wide. Occipital ring is longest (sag.) behind central glabellar area, narrows considerably behind lobe 1p, gently convex in profile, more strongly arched transversely. Occipital furrow V-shaped, well incised - especially distally. Lateral glabellar lobe 1p is subquadrangular to subrectangular in outline, not as wide as central area of glabella from which it is separated by a shallow furrow. Main branch of lateral furrow 1p swings inwards and progressively more backwards; a short anterior branch runs forwards over inner side of subcircular lobe 2p which is conspicuously shorter (exs.) than palpebral lobe. Lateral furrow 2p is deep, transversely directed, connects with anterior branch of furrow 1p. Lateral lobe 3p is transversely elongate, lateral furrow 3p is distinct. Many specimens (for example PMO 81138, Pl. 6 fig. 8) show evidence of a fourth lateral furrow low down on side of glabella trending towards anterior pit. Frontal lobe typically has rounded anterolateral corners but a somewhat flattened (tr.) anterior margin. In lateral profile glabella is horizontal until lobe 2p after which it is mildly convex, falling moderately steeply to preglabellar furrow.

Axial furrow deep beside lobe 1p, becomes less so towards anterior pit and below side of frontal lobe. Preglabellar area about as long (sag.) as occipital ring. In lateral aspect the dorsal surface of anterior border is somewhat convex (sag.) and less steeply inclined than the anterior side of preglabellar furrow; outer side of anterior border is convex down to rostral suture. In dorsal view anterior margin is gently convex forwards; in frontal view it is gently to moderately arched, losing height abaxially towards facial suture.

Posterior border is convex and noticeably increases in width (exs.) from axial furrow to fulcrum, from fulcrum becomes flatter and wider abaxially but narrows slightly just before meeting facial suture due to forward swing of posterior margin.

Posterior border furrow and posterior branch of facial suture are as in F. jemtlandica (compare Pl. 4, fig. 8 with Pl. 6, fig. 8). Anterior branch of facial suture is more or less straight, runs forwards and inwards to anterior margin. Mid-point of weakly convex (tr.) palpebral lobe varies from opposite posterior half of lobe 2p (PMO 81250, Pl. 6, fig. 1), or even fractionally more forwards (PMO 81138, Pl. 6, fig. 7), to outer part of furrow 1p (PMO 5491, Pl. 6, fig. 9); it slopes steeply adaxially and is not confined by palpebral furrow but there is a break in slope on reaching inner part of fixed cheek; it is almost as long (exs.) as lobe 1p. Anterior part of fixed cheek descends steeply to very shallow outer extension of preglabellar furrow.

Border sector of rostral plate and hypostome are essentially as in F. jemtlandica.

Thorax known only from isolated segments. Axial ring fairly convex (sag.), widens (exs.) and is mildly inflated near axial furrow. Articulating half ring is three quarters as wide (sag.) as axial ring, narrows gradually distally; articulating furrow is U-shaped, narrows sharply abaxially. From axial furrow to fulcrum posterior band of pleura is higher and about twice as wide as anterior band, it continues distally to form bounding rim to pleural facet. Articulating shelf runs along anterior margin of pleura. U-shaped pleural furrow narrows gradually to flat pleural facet where it swings forwards, then backwards, before dying out.

Pygidium is about twice as wide as long. Axis has five to seven axial rings. First five ring furrows are complete though furrows three to five become progressively effaced medially. Sixth and seventh ring furrows not always present. Axial furrow weakest around terminal axial piece. Pleural region has five pleural and five slightly longer interpleural furrows, the latter reaching the lateral margin. A very short (sag.) postaxial sector falls steeply from axial furrow.

Ornamentation on glabella is dominated by coarse, irregularly shaped, closely spaced tubercles though all sizes down to the finest are present. Largest tubercles, which are often pierced by a hole, are most evident on occipital ring and central area of glabella between lobes 1p and 2p. Fine to medium sized tubercles cover inner part of fixed cheek and anterior border. Abaxial part of fixed cheek covered with fine tubercles. Tubercles on free cheek are of three main types: On adaxial part below eye socle they are generally rounded and fine to medium in size; approaching and covering lateral border furrow there are closely spaced granules; on lateral border the tubercles become larger again but here, except near genal angle, they are oval and scale-like, their long axes running parallel with lateral margin. Tubercles on border sector of rostral plate similar to lateral border, some are perforate; a row of finer tubercles runs along the inner arc. Hypostome and pygidium covered with granules and rounded tubercles except for maculae and deepest parts of all furrows.

DISCUSSION. The palpebral lobe of this species varies in position as was related in the generic discussion. The rather flat outline to the frontal glabella lobe reaches an extreme in some cranidia (PMO 5491, Pl. 6, fig. 9) where it is straight and transversely directed. All specimens show a slight swelling of the anterior border (thus producing a gradual change of slope of the preglabellar area as seen in profile); in the holotype it is pronounced and approaches the condition seen in Flexicalymene (Reacalymene). Though it is otherwise ill-preserved, a cranidium referred by Thorslund (1940, p. 147, pl. 12, fig. 21) to F. jemtlandica also exhibits a somewhat convex anterior border, and I have questionably placed it, and a pygidium from the same locality (Thorslund 1940, pl 12, fig. 22), in the synonymy of scabustula. Changes in the pygidial morphology of scabustula during growth are similar to those observed in jemtlandica (compare Pl. 7, figs. 15 and 10 with Pl. 5, figs. 5 and 4).

Apart from the sagittally convex nature of the anterior border, F. scabustula differs from F. jemtlandica through its straighter anterior branch of the facial suture and in particular its glabellar ornamentation (Pl. 5, figs. 10, 11). The glabellar tubercles are considerably larger, more numerous and closer together than in jemtlandica, and the ornamentation of scabustula is so distinct that it immediately differentiates the new taxon from all other closely related species. A further difference is that in lateral profile the glabella of jemtlandica falls evenly from the occipital furrow to preglabellar furrow, whereas that of scabustula exhibits a faint break of slope between the horizontal posterior and descending anterior parts (compare Pl. 6, figs. 4, 6 with Pl. 4, figs. 4, 6). Many specimens of scabustula have quite a strongly arched anterior cranidial margin when seen in frontal view (Pl. 6, fig. 7). This tendency has not been observed in jemtlandica but it is an inconsistent feature of the new species and can not always be used to separate the two taxa.

All the British species in the onniensis group have finer glabellar tubercles.

OCCURRENCE. In addition to the type locality where it is most common, it also occurs in the Upper Chasmops Limestone (4b δ) at Bygdøy, Rambergøya, and Land Steilene (Oslofiord) in the Oslo-Asker district. Perhaps also from the Upper Chasmops Limestone, autochthonous beds, Slandrom, Jämtland, Sweden (see discussion).

Flexicalymene cf. F. scabustula sp. nov.

Plate 8, fig. 10

MATERIAL. Two incomplete cranidia, PMO 5285, PMO 20399; both collected 1903.

OCCURRENCE. Lower Chasmops Limestone (4b β), NW Lindøya, Oslofiord, Oslo-Asker district.

DISCUSSION. This species is the only calymenid the author has seen from the Lower Chasmops Limestone. Although incomplete, sufficient remains of one of the cranidia (PMO 20399) to suggest it is closely related to F. scabustula sp. nov. The coarse glabellar tubercles and characteristic glabellar profile of the new species are both displayed by this specimen (compare Pl. 6, fig. 7 with Pl. 8, fig. 10). The position of the palpebral lobe is difficult to determine as it is represented only in the internal mould form, but it seems to be centred opposite the posterior part of lateral glabellar lobe 2p. F. scabustula would have a relatively long stratigraphical range if future collections confirmed the existence of the species at this horizon.

<u>Flexicalymene</u> sp. indet 1

Plate 8, figs. 6, 8, 9, 11

MATERIAL. One external mould of an incomplete cranidium, PMO 81641, coll. P. Wendilbo, 1952; one external and one internal mould of a partial cranidium and pygidium, PMO 81678, PMO 81679, coll. N. Spjeldnaes, 1950.

OCCURRENCE. PMO 81641 is from the Lower <u>Chasmops</u> Shale(4bα) of Blommenholm, Baerum, Oslo-Asker district. PMO 81678 and PMO 81679 are from the Lower <u>Chasmops</u> Shale of N Hvalstad, Oslo-Asker district.

DESCRIPTION. Basal glabellar lobe is quadrangular in outline. Lateral furrow 1p is deep. There is a suggestion on one specimen (PMO 81641, Pl. 8, figs. 9, 11) of a very small intermediate lobe. Lateral lobe 2p is at least half as large as lobe 1p, elongate (tr.), slopes downwards and outwards to axial furrow. Lateral furrow 2p is well marked. Lobe 3p is of similar shape to lobe 2p and confined anteriorly by a sharply incised furrow 3p. A short (tr.) but definite furrow 4p runs up side of glabella from near the anterior pit. Incomplete anterior border is steeply upturned (PMO 81641) though the amount of inclination may have been affected by distortion. Palpebral lobe apparently centred opposite lateral glabellar lobe 2p. Surface of cranidium (exceptfurrows) covered with circular tubercles of varying size, many of which are perforate.

Pygidium has at least five axial rings. Five pleural and five interpleural furrows are present on the pleural region; the interpleurals are best marked distally.
Most of this description is based on PMO 81641.

DISCUSSION. The incomplete and distorted nature of this material does not permit recognition beyond generic level. The large basal and 2p glabellar lobes of the better preserved cranidium (PMO 81641) are similar to those found in F. acantha Bancroft, 1949 from the Costonian of Shropshire but in that species the lateral lobe 3p is proportionately smaller and Dean (1963, p. 216) has noted that the "external impression of the test", where available, "is seen to be practically smooth".

On the basis of the extant Norwegian specimens it would be unwise to attempt a detailed comparison with other taxa and at present it is sufficient to record the genus from the Lower Chasmops Shale of the Oslo-Asker district. Together with the single cranidium referred to Flexicalymene cf. caractaci, the material in question represents the first appearance of Flexicalymene in the Middle Ordovician of Norway.

Flexicalymene sp. indet. 2

Plate 8, fig. 12

MATERIAL. Four internal moulds of incomplete cranidia, PMO 81528, PMO 91011-91013; coll. N. Spjeldnaes, 1950.

OCCURRENCE. All the cranidia are from the Upper Chasmops Shale ($4b\gamma$) of N Hvalstad, Oslo-Asker district. PMO 81528 is from the strophomenid layer, and PMO 91011-91013 from the calymenid layer.

DISCUSSION. This material, of which the best cranidium is figured, is too incomplete and crushed for specific determination. The position of the palpebral lobe is centred opposite lateral glabellar lobe 2p; there is a small intermediate lobe within the fork of furrow 1p, and the glabella extends as far forward as the fixed cheek. After allowing for distortion, the general shape of the glabella is quite similar to that of F. caractaci and the age of the Norwegian specimens is approximately the same as the British species.

Flexicalymene sp. indet. 3

Plate 6, fig. 13

MATERIAL. One cranidium, PMO 81251; coll. Bockelie & Nikolaisen, 1966.

OCCURRENCE. Upper Chasmops Shale (4bγ), Hestesund, Landøya, Oslo-Asker district.

DESCRIPTION. Glabella rather wide at subquadrate basal lobes. Side of central glabella area gently swollen at inner end of furrow 1p. Lobe 2p bounded adaxially by shallow furrow. Furrow 2p deep. Lobe 3p transversely elongate, runs down side of glabella. Furrow 3p distinct. Very short, weak furrow 4p ascends lower side of glabella from posterior part of anterior pit. Anterior border slopes upwards moderately steeply from preglabellar furrow. Anterior margin gently arched forward. Middle of palpebral lobe opposite posterior part of lobe 2p or furrow 1p.

DISCUSSION. The rather broad nature of the posterior part of the glabella in this specimen appears to a large extent to be due to compression which has also resulted in the cranidium being severed and thus adding to the effect. The position of the palpebral lobes emphasizes the difficulty of making a distinction between Flexicalymene and Onnicalymene in material which has been somewhat distorted. On the right side of the cranidium the limits of the palpebral lobe stretch from lateral furrow 2p to the anterior corner of lobe 1p with the mid-point lying opposite the posterior half of lobe 2p. The palpebral lobe is incomplete on the left side, but its mid-point is seen to be farther back, opposite lateral furrow 1p.

Of the Norwegian species of Flexicalymene this Upper Chasmops Limestone specimen is possibly closest to F. scabustula sp. nov. (compare Pl. 6, fig. 9). Much of the cuticle is missing from the median glabellar lobe and on the rest of the surface most of the ornamentation has been effaced but the overall form of the glabella (particularly in profile) and anterior border suggest this comparison. Also, it is similar to the cranidium referred to F. cf. F. scabustula from the Lower Chasmops Limestone (Pl. 8, fig. 10) and is intermediate in age between that specimen and the new species.

Subgenus Flexicalymene (Reacalymene) Shirley, 1936

TYPE SPECIES. Reacalymene limba Shirley, 1936, p. 409, pl. 29, figs. 11, 12; from the Soudleyan Stage (Caradoc), Bala area, N Wales. By original designation of Shirley 1936, p. 395.

DISCUSSION. In 1936 Shirley established the genus Reacalymene which he distinguished from Flexicalymene on the basis of the anterior border being marked from the preglabellar furrow by a ridge. Subsequent workers (Whittington 1954, p. 148, in Moore 1959. p. O452, 1965, p. 58; Dean 1962, p. 112) have encountered difficulty in the use of this one character to separate the two taxa due to discrepancies in the prominence of the ridge between internal and external mould specimens. Even where the ridge is distinct, the great similarity of the other exoskeletal characters of Reacalymene to those of Flexicalymene is unquestionable. As a consequence Reacalymene is now generally regarded as a subgenus of Flexicalymene. Variation in the anterior border of F. scabustula has already been noted (see discussion of that species), but in scabustula the break in slope between anterior border and preglabellar furrow is gradual, whereas in members of Reacalymene the change is rather more sharp and thus the division between furrow and border better defined. The form of the preglabellar area of the Norwegian cranidium described below accords best with that found in F. (Reacalymene) and I have therefore referred it to this taxon. Nevertheless it is clear there is little difference between F. (Flexicalymene) and F. (Reacalymene) and it is most unlikely that members of the latter represent an evolutionary lineage separate from the nominate subgenus.

Flexicalymene (Reacalymene) sp. nov.

Plate 8, figs. 1-4

MATERIAL. One incomplete cranidium, PMO 69372; coll. L. Størmer.

OCCURRENCE. Upper Chasmops Limestone (4b δ), 0-1 metre in the profile, Ballangrud, Hadeland.

DESCRIPTION. Lateral lobe 1p quadrangular. Lateral furrow 1p narrow and deep between first two lateral lobes, at median glabellar lobe bifurcates, anterior branch crossing inner neck of ovate lobe 2p, posterior branch turning sharply back towards occipital furrow. Small intermediate lobe between these two branches. Lobe 3p about half as large as lobe 2p. Lobe 4p small, furrow 4p weak. Frontal lobe has rather well rounded antero-lateral margins; anterior margin blunt, falls but a short distance to preglabellar furrow, does not quite reach as far forward as anterior part of fixed cheek. Dorsal surface of glabella descends gradually forwards from occipital furrow (Pl. 8, fig. 2).

Axial furrow deepest around lobe 1p, shallows anteriorly but is of about constant width to anterior pit at side of frontal lobe. Preglabellar furrow about as wide (sag.) as axial furrow, steps up on anterior side into longer, horizontally inclined anterior border. Weak ridge between anterior border and preglabellar furrow marked only in front of frontal glabellar lobe. Outer side of anterior border exceedingly narrow (Pl. 8, fig. 4). Anterior margin (dorsal view) and rostral suture (frontal view) weakly arched forward and upward respectively. Palpebral lobe mid-point sited opposite posterior part of lobe 2p. Posterior branch of facial suture directed transversely from eye lobe before turning obliquely backwards to cross lateral border furrow, it then runs exsagittally and finally curves outward again to posterior margin (Pl. 8, fig. 3).

DISCUSSION. The author has seen only one specimen of this species from the Upper Chasmops Limestone though it is quite abundantly represented in the Lower Tretaspis Shale ($4c_{\alpha}$) of the Oslo Region. Material from the latter, slightly later horizon will be described elsewhere and used as a basis for formally erecting the taxon. The above description is based solely on the one cranidium from Hadeland.

This cranidium of F. (Reacalymene) sp. nov. is distinguished from the type species, F. (R.) limba, by having less strongly convergent cranidial axial furrows, a straighter (tr.) less rounded anterior margin to the frontal glabellar lobe, a small 4p lobe and 4p furrow, and no marked widening of the axial furrow outside lobe 1p (compare with Whittington 1965, pl. 16, figs. 14-17). Other differences exhibited by material of F. (Reacalymene) sp. nov. from the Lower Tretaspis Shale include a relatively narrower thoracic axis and distinct interpleural furrows on the pygidium. The Norwegian cranidium differs from F. (R.) pusulosa Shirley, 1936 from the Costonian of Shropshire in having a marginally shorter glabella, a 3p furrow which reaches the axial furrow, a much less transversely elongate lobe 2p, and a relatively narrower (tr.) median glabellar lobe. It may also be noted that F. (R.) pusulosa and F. (R.) limba both lack an intermediate lobe at the inner end of furrow 1p; this lobe is present on the cranidium described above but it is not a consistent feature of conspecific specimens from the Lower Tretaspis Shale. F. (R.) croneisi (Roy, 1941) from the Ordovician (? Lower Cincinnatian; see Whittington 1954, p. 121) of Sillimans Fossil Mount, Baffin Island is easily separated from the Norwegian species by its more anteriorly positioned eyes which are centred opposite the posterior part of lobe 1p (see Whittington 1954, p. 147, pl. 62, figs. 13-15).

GENUS Gravicalymene Shirley, 1936

TYPE SPECIES. Gravicalymene convolva Shirley, 1936, p. 395, pl. 29, figs. 16-18; from the Birdshill Limestone, Pusgillian, Birdshill Quarry, near Llandeilo, Wales. By monotypy.

Gravicalymene capitovata sp. nov.

Plate 9, figs. 1-8, Plate 10, figs. 1, 5-9, 11, 12

? 1953 Calymene; Størmer, p. 79.

DERIVATION OF THE NAME. From the Latin, capitaneus, chief in size, and ovatus, egg-shaped, referring to the nature of the basal (1p) lateral glabellar lobes

HOLOTYPE. Internal mould of an incomplete cranidium and its counterpart; PMO 91061-2; coll. by Dr. D.L. Bruton, 8.6.71; Pl. 9. figs. 1-4, 6-8. In juxtaposition to the holotype cranidium there is a pygidium and part of a thorax; these may well belong to one disarticulated specimen.

TYPE STRATUM AND TYPE LOCALITY. Ogygiocaris Shale ($4a\ \alpha_3$), the scree from the road cutting at Muggerudkleiva, Eiker-Sandsvaer district. I am informed (Dr. D.L. Bruton, pers. comm.) that although most of this scree material belongs to the division $4a\ \alpha_3$, one cannot exclude the possibility that some blocks from higher beds ($?4a\ \alpha_4$) have also been mixed.

ADDITIONAL MATERIAL. One internal mould of an almost complete cranidium, PMO 82681; eleven internal moulds of incomplete cranidia, PMO 60414, PMO 60418 (3 specimens), PMO 66598 (2 specimens), PMO 91032-33, PMO 91043, PMO 91060, PMO 91064; one internal mould of an incomplete cranidium and counterpart, PMO 91047-48; three external moulds of incomplete cranidia, PMO 60421, PMO 91042, PMO 91045; four internal moulds of free cheeks, PMO 91034, PMO 91036, PMO 91055, PMO 91063; one external mould of an incomplete free cheek, PMO 91037; three external moulds of rostral plates, PMO 91036 (two specimens), PMO 91056; two hypostomes, one complete together with counterpart, PMO 91051-52, the other an incomplete external mould, PMO 91038; two internal moulds of pygidia, PMO 91039, PMO 82705; three internal moulds of pygidia and their counterparts, PMO 60404, PMO 60410, PMO 91058-59, PMO 91049-50.

DIAGNOSIS. Glabella strongly bell-shaped in outline. Ovate lateral glabellar lobe 1p is about three times as large as lobe 2p.

Frontal glabellar lobe lies behind anterior part of fixed cheek. Anterior border slopes steeply forwards and upwards from near vertical anterior face of preglabellar furrow. Strong trace of eye ridge on abaxial side of axial furrow opposite lateral glabellar furrow 2p. Inner, anterior part of fixed cheek somewhat inflated and overhanging. Narrow, rille-like posterior border furrow. Abaxial part of fixed cheek slopes steeply downwards (tr.). Pygidium has six complete, two incomplete axial rings and six pleural furrows.

DESCRIPTION. Holotype cranidium just less than half as long (sag.) as wide. Glabella about as long as wide, strongly bell-shaped in outline. Occipital ring about one quarter times as wide (sag.) as long, of constant width abaxially to lateral lobe 1p then gradually narrows to axial furrow. Occipital furrow is a narrow straight (tr.) groove which is fairly shallow across central glabellar area, deepens rapidly swinging backwards behind lobe 1p. The latter is very large, ovate, with a well rounded abaxial margin and slightly pointed anterior margin. Lateral furrow 1p deep at axial furrow, shallows as it curves inwards and strongly backwards. A shallow, exsagittally directed depression connects furrow 1p to occipital furrow. Lateral lobe 2p subcircular, only one third as long as lobe 1p and semi isolated from median lobe. Lateral glabellar furrow 2p confined to dorsolateral glabellar surface. Lateral lobe 3p very small; lateral furrow 3p weakly developed, not observed in dorsal view. Frontal glabellar lobe very gently arched forwards, slightly overhangs preglabellar furrow, is level in length with inner corner of fixed cheek, but well behind most anterior part of this cheek.

A deep, narrow (sag. & exs.) preglabellar furrow rises vertically to meet anterior border which proceeds forwards and steeply upwards before turning sharply over at anterior margin. In dorsal view anterior border is of similar outline to rostral plate, though less convex forwards. Axial furrow is deep and most narrow around lateral lobe 1p, slightly wider opposite lobe 2p, but constricted in width and depth opposite lateral furrow 2p where eye ridge runs down abaxial side and across the base of the furrow; in front of furrow 2p it is about same width as preglabellar furrow. Anterior pit in base of axial furrow below lateral furrow 3p.

Posterior margin of fixed cheek is transversely directed to fulcrum, then turns more backwards to genal angle. Posterior border narrow and moderately convex (exs.) to fulcrum, becomes wider and flatter towards facial suture. A moderately deep rille-like posterior border furrow is constantly narrow throughout its length (tr.). Posterior part of fixed cheek slopes gently downwards from axial furrow to just past fulcrum, thereafter much more strongly to facial suture. Inflated anterior part of cheek distinctly overhangs narrow (exs.), forward and outwardly directed continuation of preglabellar furrow (Pl. 9, fig. 3). Mid-point of palpebral lobe lies opposite anterior part of 2p lobe. Posterior branch of facial suture runs for a short distance outwards then bends backwards to meet weakly developed abaxial part of posterior border furrow, finally turns more posteriorly to join posterior margin. Anterior branch of suture progresses forwards and inwards to anterior margin. Convexity of inner part of free cheek and width of lateral border both decrease posteriorly.

Border sector of rostral plate is about one third as long as wide. Rostral suture moderately well arched. Connective suture swings slightly inwards near junction of border and doublure sectors. Narrow (sag. & exs.) anterior border of hypostome is flexed ventrally. Anterior border furrow almost extinct. Moderately large anterior wing has ventral pit. Lateral border shows marked expansion in width and decrease in convexity behind posterior lobe of median body and is produced into a flat, long fin-like projection. Lateral border furrow shallowest at mid-length. Gently convex (sag. & Tr.) anterior lobe of median body has no central projection; crescent shaped posterior lobe falls quite steeply to very short (tr.) border furrow. Median furrow barely distinguished; maculae apparently absent though preservation of material not good.

Partial thorax shows moderate inflation of axial ring at axial furrow. Axis of pygidium has six complete and two incomplete ring furrows, the last two present on terminal axial piece. Seventh ring furrow is lacking medially, thus broken into two sections each of which fails to reach axial furrow. Eighth ring furrow confined to central two thirds of axial width, does not reach axial furrow. The latter is shallowest anteriorly, its two sides converge posteriorly until fourth ring furrow, becomes more incised and subparallel thereafter to sixth ring furrow, finally swinging inwards, maintaining depth around terminal axial piece. Six well marked pleural furrows, the first of which crosses articulating facet, almost reach lateral margin. Less distinct, slightly longer interpleural furrows become better marked abaxially.

Glabella, posterior part of fixed cheek and pygidium (excluding furrows) have scattered tubercles which are much finer than those on the inner anterior part of fixed cheek and anterior border. On available specimens ornament of rostral plate and hypostome is ill-preserved, but both display a few fine granules and small tubercles.

DISCUSSION. G. capitovata represents the earliest member of the family from Norway; the occurrence of Gravicalymene in Norwegian rocks of pre-Caradocian age was somewhat unexpected. It is the stratigraphically earliest species assigned to this genus but there is evidence to suggest Gravicalymene existed even earlier, in Lower Llanvirn times. Hughes described a new species of Flexicalymene of this age, F. aurora, from the Builth Inlier. The holotype (Hughes 1969, pl. 9, fig. 4) has a subtrapezoidal glabellar outline but in the paratype (Hughes 1969, pl. 8, fig. 7) the glabella is strongly bell-shaped - the same as in Ordovician species of Gravicalymene. Also the frontal glabellar lobe of the paratype seems to project further anteriorly and the 2p lobe be relatively smaller than that of the holotype, but both specimens are from the same horizon and locality and are perhaps best regarded as conspecific. The preglabellar area of aurora is unknown though the subquadrate form of the glabella in front of lobe 2p in both holotype and paratype is characteristic of Gravicalymene rather than Flexicalymene. Hughes recognised the square anterior of the glabella in aurora provided a basis for specific distinction within Flexicalymene but this species seems better accommodated within Gravicalymene.

G. capitovata is readily separated from all other Gravicalymene species by the shortness of its glabella relative to the length of the fixed cheek, the great difference in size between lateral glabellar lobes 1p and 2p, and the constantly narrow (exs.), rille-like posterior border furrow. Together with aurora, this includes the following British forms: G. praecox (Bancroft, 1949) from the Harnagian of Shropshire, G. inflata Dean, 1963 from the Onnian of Shropshire, G. jugifera Dean, 1962 from the Pusgillian of the Cross Fell Inlier, and G. convolva Shirley, 1936 from the Pusgillian of the Llandeilo area, Wales. In addition, G. jugifera has a wider (sag.) preglabellar furrow and narrower (sag.) anterior border; G. convolva has a narrower, more dorsally convex (sag.) and horizontally projecting anterior border, and G. inflata has a straight (tr.), narrow anterior border. The latter species shows a likeness to G. capitovata because of its rather inflated fixed cheeks. The distinct eye ridge on the side of the axial furrow is characteristic of the Norwegian species, though the holotype of G. praecox (BM In42090) also exhibits a constriction of this furrow opposite lateral lobe 3p.

Gravicalymene species from the Middle and Upper Ordovician of Kentucky (Ross, 1967) are perhaps closer than the British to capitovata. In particular Gravicalymene sp. 3 of Ross (1967, pl. 2, figs. 24-27) which has a steeply inclined anterior border and a somewhat short glabella. It is distinguished, however, by its narrower anterior border, wider preglabellar furrow, and deficiency of eye ridge in the axial furrow. G. hagani Ross, 1967 from Kentucky, and G. quadricapita (Stumm & Kauffman, 1958) and G. praelongicephala (Stumm & Kauffman, 1958) from Michigan all differ, amongst other things, in the form of the posterior border furrow, length of the glabella relative to the fixed cheek, and size of 2p lobe. The cranidium described as Gravicalymene aff. G. quadricapita by Ross (1967, pl. 4, figs. 14, 15) has the remnant of an eye ridge on the side of the axial furrow, but here it is opposite the third glabellar lobe.

Whittington (1971, p. 131) concluded that his monotypic genus Thelecalymene from the Maquoketa Shale, Iowa was most closely related to Gravicalymene. A comparison of G. capitovata with Thelecalymene mammillata (Hall, 1861) supports this contention. The very large, ovate, basal glabellar lobe, eye-ridge in the axial furrow, overhanging anterior corner of the fixed cheek and short glabella make capitovata more reminiscent than any other Gravicalymene of T. mammillata. In contrast, the narrow (exs.) posterior border furrow of the Norwegian species is unlike Thelecalymene or, with one possible exception, other Gravicalymene species and recalls instead Pharostoma (compare Pl. 9, fig 1, with Pl. 2, fig. 8) or Platycalymene Shirley, 1936 (see Hughes 1969, Pls. 10-13). The specimen referred to by Shirley (1931, p. 31, pl. 2, fig. 11) as Calymene quadrata? King, 1923 from the Llandeilo Series of S Wales also has a very narrow posterior border furrow, and may belong in Gravicalymene (Dean 1962, p. 227).

The hypostome of G. capitovata is like that of Thelecalymene, Flexicalymene and Platycalymene species in lacking a raised area on the anterior lobe of the median body, though its posterior spines are unusually long and wide. A knowledge of the hypostomes of other Ordovician Gravicalymene species is needed to determine the value of the posterior spines in discriminating Gravicalymene from these other Ordovician genera. The very long anterior border on the hypostome of Platycalymene (see Hughes 1969 pl. 10, figs. 7, 8) is clearly different to that of G. capitovata and species of Flexicalymene. As regards the rostral plate, the doublure sector in G. capitovata is more strongly arched and the connective sutures less strongly convergent than those of F. jemtlandica or F. scabustula. Cephalic sternites may eventually prove useful in differentiating Gravicalymene from other non-buttressed Ordovician genera.

OCCURRENCE. All specimens except one come from the type locality. PMO 66598 (Pl. 10, fig. 8) comprises two cranidia from the Endoceras layer ($4a_{\alpha}$), 24.5m from the bottom of the profile of the waterfall in Ravalsjøriver, Flatla, Hedenstad, Øvre Sandsvaer. Although it is not certain, these specimens in all probability represent those referred to by Størmer (1953, p. 79) as "Calymene".

Størmer regarded the 24.5m level at Flatla as belonging to the Upper Didymograptus Shale ($4a\alpha_{1-2}$). If this is correct, the horizon is earlier than strata at the type locality.

Gravicalymene aff. G. capitovata sp. nov.

Plate 10, fig. 4

MATERIAL AND OCCURRENCE. One external mould of an incomplete cranidium, PMO 81575; from "the Shales" (Lower Chasmops Shale ?), the new road, 30-50m N of Montebello station, Ullern, Oslo district; coll. J.A. Dons, 1944. Two small distorted internal moulds, one a pygidium, PMO 81776, the other a cranidium, PMO 81779, from the "Lower Chasmops division", on the road between Opjorden and Trengen, Sandsvaer district; coll. A. Heintz, 1945.

DESCRIPTION. Glabella is strongly bell-shaped in outline. Lateral lobe 1p is elongate (exs.) and about three times as large as circular lobe 2p; lateral lobe 3p is very small. Frontal glabellar lobe well rounded in outline, lies just behind anterior part of fixed cheek. Preglabellar and axial furrows both deep and narrow; the latter with the trace of an eye ridge on abaxial side opposite anterior part of lobe 2p. Anterior border short, very steeply sloping. Posterior border furrow moderately deep and constantly narrow from axial furrow to fulcrum; abaxial part of cheek not preserved. Tubercles on cranidium are fine and closely spaced.

DISCUSSION. The description was based on PMO 81575 (Pl. 10, fig. 4); the other cranidium (PMO 81779) is much smaller and more distorted but probably belongs to the same species. The nature of the glabella, lateral lobe 1p, posterior border furrow and eye ridge clearly ally this species with Gravicalymene capitovata sp. nov. It appears to depart from the new species in the following respects: a shorter anterior border (sag. & exs.), more rounded frontal lobe, more narrowly separated (tr.) palpebral lobes, and the lack of larger tubercles on the anterior part of fixed cheek and anterior border. These specimens may represent a separate species, but due to distortion the value of some of the distinctions is put in question, and there is need of better preserved material to resolve the problem.

Some doubt exists as to the age of the specimens but they probably come from the Lower Chasmops Shale, that is in younger strata than that containing G. capitovata.

Gravicalymene? sp. indet.

Not figured

MATERIAL. One poorly preserved internal mould of a cranidium and its counterpart, PMO 81674-75; coll. N. Spjeldnaes, 1950.

OCCURRENCE. Contained in a loose block, probably from the Lower Chasmops Shale (4bα), the tunnel at Billingstad station, Oslo-Asker district.

REMARKS. This very poorly preserved internal mould has a bell-shaped glabella and ridged anterior border characteristic of both Gravicalymene and Diacalymene. There does not seem to be a genal buttress, which would suggest it belonged within Gravicalymene, though in this region of the cheek the cranidium is much distorted. Its stratigraphical position is more in keeping with the known range of Gravicalymene, Diacalymene not having been recorded below the Ashgill.

Genus QUADRICALYMENE gen. nov.

DERIVATION OF THE NAME. From the Latin, quadra, a square; referring to the shape of the glabella in front of lateral lobe 1p.

TYPE SPECIES. Q. lirella gen. et sp. nov.

OTHER SPECIES. Q. aldonensis (Reed, 1935)

DIAGNOSIS. Glabella quite strongly inflated, bell-shaped in outline; anterior to lateral lobe 1p the glabellar sides are subparallel, the anterior margin of the frontal lobe is straight (tr.) or very weakly convex forwards, and the glabellar outline is subquadrate. Anterior border is low, short and weakly to moderately upturned.

DISCUSSION. The characters displayed by a new species (Q. lirella) from Norway make it difficult to assign to any established flexicalymenine genus. The glabellar outline is similar to that of Gravicalymene species, but the slightly upturned anterior border is more like that of Flexicalymene taxa - though it is much shorter than in typical members of the latter genus (cf. Pl. 4, figs. 1-9, Pl. 9, figs. 1-8, Pl. 11, figs. 1-10). The concepts of Flexicalymene and Gravicalymene as used by Ross (1967) are accepted here, the Norwegian species is therefore excluded from both these genera, and is made the type species of Quadricalymene gen. nov. The new genus is believed to be more closely related to Gravicalymene than to Flexicalymene. The inflation and outline of the glabella in both Gravicalymene and Quadricalymene (and in the case of Gravicalymene the nature of the preglabellar area) is reminiscent of that in Protocalymene Ross, 1967 (cf. Ross 1967, pl. 9, fig. 1; 1970, pl. 18, fig. 2 with Pl. 9, fig. 1, Pl. 11, fig. 1 herein).

Calymene (Colpocoryphe ?) aldonensis Reed, 1935 is clearly congeneric with Q. lirella.

OCCURRENCE. Ampyx Limestone, Ogygiocaris Beds, Oslo Region; Didymograptus superstes Shales, Girvan district.

<u>Quadricalymene</u> <u>lirella</u> gen. <u>et</u> sp. nov.

Plate 10, figs. 2, 3, 10; Plate 11. figs. 1-10.

DERIVATION OF NAME. Diminutive of the Latin, <u>lira</u>, ridge thrown up by the plough, alluding to a similar feature in the base of the axial furrow.

HOLOTYPE. An incomplete cranidium; PMO 81919; coll. by F. Nikolaisen, 1961; Pl. 77, figs. 1-3.

TYPE STRATUM AND TYPE LOCALITY. <u>Ampyx</u> Limestone (4aβ), W side of Bygdøy, Oslo-Asker district.

ADDITIONAL MATERIAL. Seven internal moulds of incomplete cranidia, PMO 82465-66, PMO 82528, PMO 91067-68, PMO 91072-73; two internal moulds of incomplete individuals, PMO 82467, PMO 91065; three external moulds of incomplete cranidia, PMO 91069-71; one external mould of a cranidium and attached thorax, PMO 57471.

DIAGNOSIS. Preglabellar furrow and anterior border very narrow (sag. & exs.). Margin of frontal lobe straight or at most very gently convex forwards. Mid-point of palpebral lobe opposite (tr.) posterior part of lateral lobe 2p. Eye ridge absent from palpebral lobe to axial furrow, absent or exceedingly faint down abaxial side of this furrow, is directed across (tr.) its base as a broad (exs.), distinct ridge which ends below lateral furrow 3p. Thorax has thirteen segments.

DESCRIPTION. Cranidium about two and one third times as long as wide. Glabella about as long as wide, bell-shaped in outline, its dorsal surface stands moderately well above convex fixed cheek in lateral profile. Glabellar width (tr.) at lateral lobe 1p is much greater than at lobe 2p; width at lobe 3p is only marginally less than at 2p. From lateral lobe 1p occipital ring narrows and swings slightly backwards to axial furrow. Two specimens display a small, median occipital tubercle (PMO 81919, PMO 91070); other specimens are interal moulds with occipital ring poorly preserved. Well marked occipital furrow is deepest behind moderately swollen lateral lobe 1p. The latter is less than one third, but more than one quarter as wide as glabella. From axial furrow lateral furrow 1p curves inwards and progressively more backwards, faintly extending over inner neck of lobe 1p to meet occipital furrow. Lateral lobe 2p about half as large as lobe 1p and not isolated from central glabellar lobe by a furrow. Lateral furrow 3p is short (tr.). Lateral lobe 3p is almost as long (exs.) as 2p and only slightly less inflated. Lateral furrow 3p confined to glabellar side, barely seen in dorsal view. Extremely faint trace of possible lateral furrow 4p on holotype. Frontal glabellar lobe is subrectangular in outline, projects just in front of fixed cheeks, falls very steeply to preglabellar furrow.

Very narrow (sag. & exs.) and shallow preglabellar furrow fractionally undercuts frontal glabellar lobe then inclines forwards and barely upwards into equally narrow anterior border. In internal moulds anterior border turns sharply over at anterior margin; normally, where the shell remains, it is slightly more convex (sag.). Anterior margin well below dorsal surface of frontal lobe and more strongly arched upwards in frontal view than arched forwards in dorsal view. Axial furrow widest and deepest at lateral lobe 2p due to narrowing of glabella and rise of fixed cheek respectively. Below furrow 3p, extending also below side of frontal lobe, axial furrow becomes distinctly shallowed by a broad (exs.), well developed ridge running across (tr.) its base. Very faint suggestion of eye ridge running down the lower, abaxial side of axial furrow to join this ridge. Anterior pit in axial furrow about half-way along side of frontal lobe.

Posterior border is moderately convex and narrow (exs.), becomes less convex and wider (exs.) towards suture line. Posterior border furrow relatively narrow with no marked increase in width near fulcrum; is wider and less deep in internal moulds. Mid-pointof palpebral lobe lies opposite posterior part of lobe 2p on highest part of fixed cheek. Posterior branch of facial suture runs transversely outwards before turning backwards to posterior border furrow, thereafter almost exsagittally directed to posterior margin. Anterior branch curves forwards and inwards. Rostral suture is parallel to anterior margin. External mould of rostral plate and hypostome (PMO 91065) too poorly preserved to merit detailed description, but former is composed of border and doublure sectors and latter apparently lacks raised area on anterior lobe.

Thorax and pygidium are only known from the same, ill-preserved specimen (PMO 91065). Axis of pygidium exhibits at least five rings, five pleural and interpleural furrows, the latter deepest abaxially.

The glabella, fixed cheeks, and anterior border (excluding furrows) all have relatively fine, closely-spaced tubercles.

DISCUSSION. Q. lirella shows strong affinities with Q. aldonensis (Reed, 1935) from the Didymograptus superstes Shales (= Nemagraptus gracilis Zone), of the Girvan district. Both species have the same distinctive glabellar outline, a very blunt, steeply sloping frontal glabellar lobe, and a narrow (sag. & exs.) preglabellar furrow and anterior border. The two species are also similar in age, but aldonensis can be distinguished morphologically in the following respects. It has a more posteriorly positioned eye (opposite the anterior part of the lateral lobe 1p), a well developed eye ridge between the palpebral lobe and the axial furrow - especially down the side of this furrow, and the absence of a distinct, broad (exs.) ridge running across (tr.) the base of the axial furrow. The latter distinction can not be satisfactorily accounted for by the comparatively poor state of preservation of the internal mould syntypes of aldonensis, the only specimens of the species I have seen, as one would expect the conspicuous eye ridgeto be similarly defaced.

OCCURRENCE. Apart from the holotype and one other specimen, the rest of the material comes from an arenaceous deposit in the Ogygiocaris beds at Muggerudkleiva, Eiker - Sandsvaer district. The latter specimens are associated with a trinucleid and probably come from an horizon high in division $4a\alpha_3$, or possibly $4a\alpha_4$ (see Størmer, 1953, p. 80). PMO 57471 was found in the Ampyx beds ($4a\beta$), 100 m N W of the light-house, Saltboden, Frierfjorden, Skien-Langesund district.

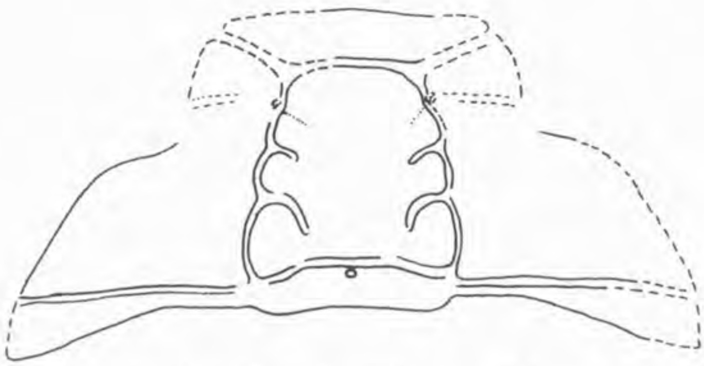
METACALYMENE Kegel, 1927, A MONOTYPIC CALYMENID FROM THE KOPANINA FORMATION (SILURIAN) OF BOHEMIA.

Bohemian calymenids of Llandovery to Ludlow age.

Compared with other areas, for example Baltoscandia or the British Isles, the family Calymenidae is ill-represented in the Lower Palaeozoic strata of Bohemia. This discrepancy is well seen during the Ordovician where only about six species, belonging mainly to Flexicalymene or Pharostoma, have been recorded from Czechoslovakia. The contrast is even more marked during the Silurian, especially from Llandovery to the end of Ludlow times; while the trilobite faunas from Gotland and Britain are relatively rich in calymenids, members of the family are rarely found in Bohemia. Apart from Diacalymene diademata (Beyrich, 1846) from high in the Liten-Schichten (= high Wenlock Series) and one other recorded but as yet unpublished Diacalymene species from beds of Llandovery age (noted by Snajdr in Trilobite News, 1971, No.1, p.16), I am unaware of any other calymenid from the Bohemian Llandoverian or Wenlockian. Indeed, the genus Calymene which elsewhere is so abundant, specifically diverse, and widespread during the Wenlockian is absent throughout the Liten-Schichten - beds which are correlated with all of the Llandovery and most of the Wenlock Series (Cocks, Holland, Rickards & Strachan 1971, fig. 9).

Within this somewhat atypical Bohemian region one finds Metacalymene baylei. This is an unusual species which represents a morphological anachronism in having little similarity with other Silurian taxa, while exhibiting many characters in common with those of Platycalymene Shirley, 1936, a genus occurring in the Lower and Middle Ordovician of Britain and Scania. M. baylei occurs only in

A. Sagittal profile. X6.



B. Dorsal outline. X6.

Text fig.1.

P. duplicata (Murchison)
Sularp Shale
Rävatofta
near Röstånga
Scania.

the Kopanina Formation of Bohemia which is correlated with the British Ludlow Series and the last graptolite zone (M. ludensis) of the Wenlockian (Cocks et al. 1971, fig. 9). In particular it is associated with the lower Ludlow horizon in the Kopanina Formation that yields Cromus beaumonti (Barrande, 1846).

Historical survey of Calymene baylei Barrande, 1846.

Barrande erected Calymene baylei in 1846 and in the first part of his monograph (1852) described it more fully and commented on the likeness of his taxon with the species described by Murchison (1839, p.661, pl. 25, fig. 8) as Asaphus duplicatus (= Platycalymene duplicata (Murchison, 1839)) from the Middle Ordovician of Wales. Salter (1865, p. 101) also noted the resemblance between the two species but it was not until 1927 when Kegel erected Metacalymene as a subgenus of Calymene that Murchison and Barrande's taxa were united in a separate higher category. Kegel designated C. baylei as the type species of his new subgenus which was founded on the rather low or depressed nature of the exoskeleton, the flat area in front of the glabella which in part comprised a flat anterior border, and the almost straight axial furrows.

In his revision of the Calymenidae, Shirley (1936, p. 393) suggested that C. baylei and C. duplicata were not directly related but were merely homeomorphs. He placed emphasis on the form of the preglabellar area and anterior border in his revised classification of the family and used the differing form of these characters in the two species as a basis for separation. The great time interval dividing baylei and duplicata combined with a lack of stratigraphically intermediate forms was taken as further evidence that these species were not closely related. Kegel's Metacalymene was given generic rank and left to contain only the type species, M. baylei; a new genus, Platycalymene, was created to receive C. duplicata, type species, a new species, P. tasgarensis, and P. dilatata (Tullberg, 1882) from the Middle Ordovician Chasmops Series of Scania.

Richter (1940, p. 1030) reviewed the work of Shirley and concluded, amongst other things, that he was in agreement with Kegel's concept of the subgenus Metacalymene and that further subdivision was unwarranted. In his work on the trilobite faunas of the Shelve Inlier, Whittard (1960, p. 151) maintained Platycalymene as a genus distinct from Metacalymene.

Apart from one specimen figured by Shirley in 1936 and one by Horny and Bastl in 1970, I am unaware of any other photograph of Barrande's species, though it has been depicted in the form of line drawings (Kegel 1927; Whittington in Moore 1959). This study represents the first revision of the taxon based on Barrande's material.

SYSTEMATIC PALAEONTOLOGY

Family CALYMENIDAE Milne-Edwards, 1840
Sub family FLEXICALYMENINAE subfam. nov. (herein Chapter B)
Genus METACALYMENE Kegel, 1927

TYPE SPECIES. Calymene baylei Barrande, 1846, p. 51; from the Kopanina Formation, Silurian, ? Kolednik, Bohemia. By original designation of Kegel, 1927, p. 619.

OTHER SPECIES. None known.

DIAGNOSIS. Exoskeleton generally depressed. Lacks genal buttresses, glabellar lobes non-papillate. Trapezoidal glabellar outline. Anterior border represented by very weak rim. Posterior border furrow lens-like in outline. Very gently convex (tr.) pygidial axis tapers gradually and evenly posteriorly.

DISCUSSION. A comparison of figured specimens of Metacalymene and Platycalymene, the latter having been discussed and comprehensively illustrated by Whittard (1960) and Hughes (1969), reveals well the similarity of the two taxa. Most obvious is the likeness in overall form of the exoskeleton - rather depressed and transversely wide. Metacalymene and Platycalymene lack buttresses from the fixed cheek and have non-papillate glabellar lobes; consequently it is accepted here that both genera belong to the same major evolutionary stock (Shirley 1936, p. 401). The problem lies in deciding just how closely they are related or even if the species in question represent stratigraphically isolated members of a single lineage.

Shirley (1936) differentiated Platycalymene from Metacalymene essentially on the nature of the anterior border which in the former was described as "roll-like" and in the latter as "very faint" (p.394) or lacking - "without ridge or raised rim" (p. 395). More recently Hughes (1969, p. 88) has illustrated cephalic profiles of various Platycalymene species and shown that the anterior border in his material is not so pronounced or elevated above the preglabellar furrow as in the specimen of P. duplicata (Murchison) depicted by Shirley (1936, p. 391, text-fig. 2.). Some of Hughes' profiles (especially 6J) show a weakly convex anterior border and approach the lateral profiles of M. baylei figured here (Pl. 1, fig. 2, Pl. 2, fig. 2, Pl. 3, fig. 2). The Bohemian material is well preserved. Many of the cranidia illustrated by Hughes are somewhat flattened and all are internal moulds. As the form of the anterior border is known to differ markedly between the internal and external moulds of calymenid specimens, this comparison is therefore misleading. Unflattened external moulds of Platycalymene are rare as the genus is almost totally confined to shaly facies (Shirley 1931, p. 19; Hughes 1969, p. 84), but a sagittal section through the rubber cast of a well preserved cranidium (IPLU 322; see Text fig. 1) of P. duplicata (= P. dilatata (Tullberg, 1882)) from Scania shows a more prominent anterior border than on those specimens figured by Hughes and is reasonably close to Shirley's profile drawing, though without such a steeply sloping posterior face. It is without doubt considerably more inflated and pronounced than the feeble rim which represents the anterior border of M. baylei. The difference between the anterior border of Platycalymene and that of Metacalymene may not be as great as suggested in Shirley's illustrations but it is here considered to be always sufficiently distinct to enable discrimination of the two taxa.

Another feature of the anterior border may be used to separate the Anglo-Welsh from Bohemian species. Because the border is more roll-like in Platycalymene, it occupies much more of the length of the preglabellar area than that of M. baylei; the border is never shorter than, and more often than not substantially longer than, the preglabellar furrow (see Whittard 1960, pl. 21, figs. 6, 7, 13 - 15; Hughes 1969, pl. 10, figs. 1, 5, 6, pl. 11, figs. 4, 6, 9, pl. 12, figs. 4, 5, 7, 10). In Metacalymene the anterior border is just a sagittally narrow, bounding rim to the preglabellar area, of which the border can be less than one third the total length (Pl. 3, fig. 6), though, exceptionally, in one small cranidium (Pl. 3, fig. 1) it is only slightly less than one half.

The trapezoidal glabella is similar in both Platycalymene and Metacalymene. Differences that are sometimes apparent between individual specimens of each genus (for example in the outline of the frontal glabellar lobe, shape and definition of the 3p lobe and the direction of the lateral glabellar furrow; compare P. tasgarensis Shirley in Whittard 1960, pl. 21, fig. 7 with Pl. 1 fig. 1), are not constant enough to serve for discrimination. No median tubercle has been observed on the occipital ring of Metacalymene but this feature is not always present in Platycalymene and in any case it may simply indicate a difference in sex (Hughes 1969, p. 92).

In all species assigned to Platycalymene and Metacalymene the palpebral lobe is centred opposite a point between 2p and 3p lateral glabellar furrows, though the lobe appears slightly longer in the Silurian species (compare Hughes 1969, pl. 12, figs. 4, 10, with Pl. 2, fig. 4, Pl. 1, fig. 1 respectively). The free cheek of Platycalymene with its rather sharp, narrow lateral border furrow is identical to that of M. baylei (Pl. 2, fig. 6), as is the general morphology of the fixed cheek. Nevertheless when the fixed cheek is examined in detail there is a constant difference in the form of the posterior border furrow between Platycalymene and M. baylei. In the former this furrow is equally narrow (exs.), quite deep and rille-like from the axial furrow to facial suture (see Whittard 1960, pl. 21, figs. 5 - 7, 13 - 16; Hughes 1969, pl. 10, figs. 1, 5, 6, pl. 11, figs. 6, 9, pl. 12, figs. 5, 10), whereas in the latter it is rather shallow and wide (exs.) for much of its length (tr.) and only narrows as it approaches the facial suture and axial furrow (Pl. 1, fig. 3, Pl. 2, figs. 1, 3, 4, 7, 8, Pl. 3, fig. 4). This character has not been previously employed in discriminating calymenid taxa but the constantly narrow posterior border furrow of Platycalymene is quite distinct from that of M. baylei. Hughes, (1969, p. 84), incidentally, was doubtful that the form of the anterior border alone was sufficient to maintain generic separation of Platycalymene and Flexicalymene. I know of no other species generally assigned to Flexicalymene which has the type of posterior border furrow found in P. duplicata or P. tasgarensis. If this character were combined with the form of the anterior border and depressed nature of the exoskeleton, it would probably provide a sounder diagnosis for Platycalymene. It is worthy of note that Pharostoma Hawle & Corda, 1847 and a species of Gravicalymene (to be described) from the Ordovician Ogygiocaris Shale of the Oslo Region also show a similar type of posterior border furrow to Platycalymene.

Unfortunately the rostral plate is unknown in Metacalymene and the hypostomes figured herein and by Barrande (1852, pl. 43, figs. 51, 52 - see Pl. 2, fig. 6) are unattached and merely associated with other exoskeletal remains of M. baylei. For this reason they may belong to another quite different calymenid, Calymene tenera (Barrande, 1852), which also occurs in the Kopanina Formation, and thus I have only questionably assigned the hypostome to M. baylei. In rising to a stout projection on the anterior lobe of the median body (Pl. 1, fig. 4 - projection worn off at tip) the hypostome is, in fact, decidedly more like that of Calymene s.s. and very different to that of Platycalymene (see Hughes 1969, pl. 10, figs. 7, 8) which has a substantially longer anterior border and lacks the median projection. No non-buttressed calymenid is known to have such a projection but there is the possibility it was developed by several distinct stocks during the Silurian.

The thorax is similarly constructed in Platycalymene and Metacalymene and I have been unable to discern any characters in it which would help differentiate the two taxa.

With the exception of Pharostoma foveolatum (Törnquist, 1884) from the Kullsberg Limestone of Dalarna, Sweden, the pygidia of

Platycalymene duplicata and Metacalymene baylei (together with Pharostoma simile Thorslund, 1940 from the Chasmops Limestone of Södermanland, Sweden) exhibit more axial rings and pleural furrows than any other species in the family. However, the pygidial axis in P. duplicata (and P. tasgarensis) is unquestionably different to that of M. baylei. In the Ordovician taxa the anterior part of the axis is convergent posteriorly and the posterior part is subparellel, the anterior five or six ring furrows are rather well or equally as well defined medially as abaxially, and the posterior part of the axis appears quite convex in transverse section. These features in M. baylei are, respectively, evenly tapering throughout its whole length, markedly shallower sagittally than at the apodemal pits, and very gently convex (compare Whittard 1960, pl. 21, figs. 10-12, 15, 17 and Hughes 1969, pl. 9, figs. 5, 6, pl. 10, figs. 2, 5, pl. 11, figs. 2, 5, 8, pl. 12, figs. 2, 8, pl. 13, fig. 1 with Pl. 1, fig. 3, Pl. 2, fig. 7, Pl. 3, figs. 4, 5, 7 - 9).

From this comparison it can be seen there are more differences between Metacalymene and Platycalymene than hitherto recognised. It is in the interpretation of these distinctions - whether they can only be used at the species level or whether they are significant enough to diagnose two separate higher categories - that opinion may be divided. The problem is made acute by having only one taxon in the Silurian so that it is difficult to assess if the differences observed in this are of specific or generic value.

In other calymenids the form of the anterior border has been used as a basis for generic groupings. But the value of this character as an indicator of descent may vary from group to group. Thus, although the border of M. baylei is different to that of those species assigned to Platycalymene, the overall similarity of the two taxa may provide a more reliable guide to the degree of relationship between them. Should they belong to one phyletic line, the length of time separating P. duplicata from M. baylei seems sufficient to accommodate the amount of morphological change required to derive the anterior border of the Silurian, from the Ordovician species. The absence of allied taxa in the intervening period does not support the single lineage hypothesis, though the incompleteness of the fossil record or collection failure may account for them being unknown. For the present it is considered here that the nature of the anterior border combined the form of the posterior border furrow and taper of the pygidial axis is sufficiently distinct between M. baylei and P. duplicata to uphold separation at the generic level.

Accepting Metacalymene to be a distinct stock from Platycalymene, it is still not possible to suggest whether their strong resemblance has resulted from parallel or convergent evolution as the ancestor of Metacalymene is unknown. The Bohemian Silurian offers no likely candidates. It is interesting to note that during the Ludlovian two new genera of calymenids appear apart from Metacalymene: Papillicalymene Shirley, 1936 from Gotland and Podolia and those species assigned to Spathacalymene Tillman, 1960 by Tomczykowa (1970) from Poland which I would regard as a new genus. All have a relatively restricted geographical and stratigraphical range and at most (Polish forms) contain only three species. Like Metacalymene, the origin of the Polish species is a problem, but it is reasonable to assume a derivation from Calymene for Papillicalymene (Whittington, 1971, p. 457).

OCCURRENCE. Restricted to the Kopanina Formation of Bohemia.

Metacalymene baylei (Barrande, 1846)

Plate 1, figs. 1 - 3, 6, 8, ? figs. 4, 5, 7;

Plate 2, figs. 1 - 5, 7, 8, ? fig. 6; Plate 3.

1846 Calymene Baylei. Barr.; Barrande, p. 51.

1847 C. Baylei, Barr.; Hawle & Corda, p. 87.

non 1851 Calymene baylei (Barr.); McCoy in Sedgwick & McCoy, p. 165, pl. 1, fig. 8.

1852 Calym. Baylei. Barr.; Barrande, p. 573, pl. 19, figs. 28, 29, pl. 43, figs. 49, 50, ? figs. 51, 52.

1865 Calymene Baylei, Barrande; Salter, p. 101.

1927 Calymene (Metacalymene) baylei BARR; Kegel, p. 619, 620, text-fig. 2g.

1936 Metacalymene baylei (Barrande); Shirley, pp. 393 - 95, text-fig. 2 (pars), pl. 30, fig. 1, pl. 31, fig. 6.

1940 Calymene (Metacalymene) baylei Barrande; Richter, p. 1030.

1959 Metacalymene baylei (Barrande, 1846); Whittington in Moore, p. O452, fig. 354, 2a, 2c.

1960 Metacalymene baylei; Whittard, p. 151.

1970 Metacalymene baylei (Barrande, 1846); Marek in Horny & Bastl, p. 69, pl. 16, fig. 5.

TYPE SPECIMENS. Some confusion exists in the literature over the identity of the type specimen(s). As yet this uncertainty has not been resolved but fortunately it in no way affects the status of the species.

In the recently published catalogue of type specimens of trilobites in the National Museum, Prague, Marek (in Horny and Bastl 1970, p. 69) lists only one syntype of M. baylei (NMP 624/66) - from the Kopanina Formation at Kolednik (figured here on Pl. 1, fig. 8).

However, in the same publication this specimen is recorded (by Marek, p. 69, second line) as being first used by Hawle and Corda in 1847 (p. 87). Clearly this cranidium cannot be a syntype of Barrande's 1846 species yet first used by Hawle and Corda in 1847. Neither Barrande (1846) nor Hawle and Corda (1847) figured this species so it is not possible to determine from illustrations to whom the specimen belonged, though Hawle and Corda specifically mention Kolednik as the locality where M. baylei occurs, whereas Barrande does not.

Barrande often figured the syntypes of species from his 1846 paper in 1852 but the cranidium in question is not figured, and according to the list of specimens recorded by Marek (in Horny and Bastl 1970, p. 69) no syntype(s) of M. baylei is illustrated by Barrande in this later work.

For the present I shall questionably regard the cranidium NMP 624/66 as a syntype. If it proves to be an original of Hawle and Corda (1847) and there are no other specimens which can with certainty be regarded as syntypes, there is still no need for the erection of a neotype, as in this instance the identity of the species is not in question (ICZN, Article 75 (a)(i)).

TYPE STRATUM AND TYPE LOCALITY. Kopanina Formation, Silurian, ? Kolednik, Bohemia.

ADDITIONAL MATERIAL. Numerous specimens of this taxon are present in the collections of the Narodni Museum, Prague. Several British Museums, including the British Museum, Sedgwick Museum, and Royal Scottish Museum also have a few cranidia and pygidia, as does the Riksmuseet, Stockholm. Entire individuals are rare, incomplete material is relatively common.

DIAGNOSIS. As for the genus.

DESCRIPTION. Cephalon about two and a half times as wide as long; glabella longer than wide, about three tenths as wide as cephalon. Occipital ring constantly wide (sag. & exs.) behind central glabella area, narrows gradually behind lobe 1p, at axial furrow is about half as wide as at median line and very weakly inflated; in profile it is flat or at most gently convex. Occipital furrow well marked but not very deep between basal lobes, abaxially it curves around lobe 1p and becomes substantially deeper. Subquadrate lobe 1p one third as wide as glabella, outer margin straight or gently curved, abaxial corners (especially anterior) rather angular, separated from central glabellar area by very shallow depression. Outer part of furrow 1p directed inward and slightly backward, inner part runs more sharply backward, shallows abruptly on inner side of lobe 1p. Lobe 2p subrectangular in outline, the long axis trending outward and slightly forward, isolated from median lobe by shallow furrow. Furrow 2p is a sharp, slit-like structure, deepest and widest (exs.) adaxially, in some specimens becoming rather shallow at axial furrow. Transversely elongate lobe 3p about two-thirds the size of lobe 2p, defined anteriorly by weak to moderately deep furrow 3p. In some specimens the latter barely reaches axial furrow. Extremely faint furrow 4p may be present on side of glabella running from near posterior region of anterior pit. Frontal lobe very wide (tr.) and short, anterior abaxial corners somewhat angular or may be slightly rounded, anterior margin truncate. Median glabellar lobe narrows towards occipital furrow where it is about two-thirds its width at frontal lobe, in frontal view stands above lateral lobes and in profile above fixed cheek. Dorsal surface of glabella falls gently downward from occipital furrow to lobe 3p, thereafter somewhat more steeply (though it never approaches a vertical descent) to preglabellar furrow.

Besides occipital ring shallow axial furrow runs forward and outward, is deepest around lobe 1p with a vertical outer wall, becomes progressively shallower between lobes 2p to 4p but at side of frontal lobe is indented by deep, circular, anterior pit; between frontal lobe and occipital ring axial furrow is approximately straight, trends forward and slightly inward.

Preglabellar furrow ill-defined, appears to be a narrow (sag. & exs.) very shallow depression. Preglabellar area consists of a much wider posterior part which is slightly concave upwards or flat, and inclined downward and forward or is approximately horizontal; this posterior part not a true preglabellar field as it is not defined anteriorly by what I can regard without doubt as an anterior border furrow. Anterior part or anterior border is a short (sag.), extremely low, faintly convex 'rim' which becomes narrower abaxially; outer face of border curves downward and forward to very broadly arcuate rostral suture.

Posterior margin transversely directed from axial furrow, turns obliquely backward at fulcrum, obliquely forward near genal angle. Adaxially posterior border is tightly convex and narrow, expands distally from fulcrum. Shallow posterior border furrow has considerably wider, less steeply inclined anterior than posterior slope, in outline is lens-like between axial furrow and facial suture. Fixed cheek moderately convex (exs. & tr.), from palpebral lobe gently inclined to posterior border furrow, a little more steeply to extremely weakly arcuate anterior margin. Palpebral lobe centred opposite posterior half of lobe 3p, length varies somewhat - in smaller specimens appears almost equal to that of lobe 1p, in larger specimens just greater than that of lobe 2p. Eye ridge indistinct, traverses cheek from anterior part of palpebral lobe to end just anterior to furrow 3p. Posterior branch of facial suture directed approximately transversely from eye then swings obliquely backward to cross lateral border furrow, course at genal angle unknown. Anterior branch curves forward and inward to anterior margin. Broad inner region of free cheek descends steeply from suture to shallow, narrow lateral border furrow. Lateral border also narrow, falls vertically.

Rostral plate unknown. Isolated calymenid hypostomes associated with cranidia of M. baylei may belong to this species (see generic discussion). Total length of hypostome about equal to width across reasonably large anterior wings. Anterior pit well developed. Anterior border short (sag. & exs.), flexed ventrally. Anterior border furrow scarcely impressed. Lateral border narrow (tr.), broadens behind posterior wing where posterior margin is bifid. Posterior wing flat and rather short. Median body clearly divided into two unequally long lobes by U-shaped median furrow. Anterior lobe about three times as long as posterior, subovoid in outline, strongly inflated ventrally culminating in a bluntly tipped protruberance sited towards anterior part of lobe. In profile (Pl. 1, fig. 4) anterior lobe concave between this protruberance and anterior border, gently convex down to median furrow. Posterior lobe crescent-shaped, less swollen than anterior lobe. Maculae smooth, barely convex.

Thorax (see Pl. 1, fig. 3, Pl. 2, fig. 7) depressed, has thirteen segments. Axis approximately a quarter, or slightly more, as wide as cephalon, not very convex (tr.), tapers very gradually towards pygidium. Axial rings deflected anteriorly at axial furrow and are here slightly swollen. Pleural region rather wide (tr.) and flat-topped. Posterior pleural band wider (exs.) than anterior. Pleurae bend downward some distance abaxially from, not at, fulcrum. Pleural furrow constantly deep to fulcrum, narrows thereafter, dies out on smooth articulating facet.

Pygidium just greater than twice as wide as long. Anteriorly the axis occupies about one quarter of the pygidial width, it tapers gradually and evenly throughout its length, does not quite reach posterior margin, gently convex (tr.) in section. Normally ten axial rings, sometimes nine. Ring furrows transversely directed, distinct and slit-like at axial furrow, shallow rapidly adaxially. Axial furrow rather broad, feebly marked around small terminal axial piece. In profile surface of axis inclined at about 45 degrees. Inner part of pleural region slopes gently downward; much narrower outer part almost vertically to lateral margin. Nine (occasionally eight) distinct pleural furrows fail to reach lateral margin. Interpleural furrows considerably weaker but marked throughout their length, if anything a shade deeper distally, apparently no eighth or ninth furrows developed.

Ornament on glabella, anterior border, and inner part of fixed cheek is of small to medium sized, loosely set tubercles; on outer part of fixed cheek tubercles are somewhat finer. Lateral glabellar furrow lacks tubercles; area between frontal lobe and anterior border has a few small tubercles but considerably less than glabella. Scattered tubercles on thorax. Pygidium finely tuberculate, particularly the steeply sloping outer pleural region. Many of the tubercles are perforated. In addition to these relatively larger tubercles, much of the exoskeleton is covered with extremely fine granules.

DISCUSSION. The specimens figured here are from two main sources; some were collected by the author and Dr. L. Marek in December 1971, the rest represent those figured by Barrande (1852) or are from the Barrande Collection of the Narodni Museum, Prague. It was not possible to clean any of Barrande's material, but I am most grateful to Dr. R. Horny for allowing me to prepare casts (which are illustrated here) of the originals.

Intraspecific variation is present in the presence or absence of lateral furrow 4p (Pl. 2, fig. 1; Pl. 2, fig. 3), number of axial rings and pleural furrows on the pygidium (see description and Pl. 2, fig. 7; Pl. 3, fig. 4), and relative length of the preglabellar area to that of the glabella (Pl. 2, fig. 3; Pl. 3, fig. 6).

OCCURRENCE. Known only from Kopanina Formation of Bohemia. Barrande (1852, p. 574) records the species from the following localities: Dlouha hora, Jarov (Dlouha hora), Reporyje and Ohrada. The species is apparently confined to carbonate and calcarenite facies.

The genus Diacalymene Kegel, 1927 from the Upper Ordovician and Silurian of Britain, Scandinavia and Czechoslovakia

The three species referred to Diacalymene by Shirley (1936) from the Upper Ordovician and Silurian of Britain have been examined. In addition the type species (D. diademata (Beyrich, 1846)) from Czechoslovakia has been revised for the first time, and material from Scandinavia has also been assigned to this genus. This represents the first recording of Diacalymene from Norway and Sweden. Two main groups are present within Diacalymene, the one typified by D. crassa (Shirley, 1936), the other by D. drummuckensis and D. diademata. One new species has been established. The subfamily Calymeninae Milne Edwards, 1840 is restricted herein.

SYSTEMATIC PALAEONTOLOGY

Family CALYMENIDAE Milne Edwards, 1840

Subfamily CALYMENINAE Milne Edwards, 1840

TYPE GENUS. Calymene Brongniart, 1822.

OTHER GENERA. Diacalymene Kegel, 1927; Papillicalymene Shirley, 1936, Spathacalymene Tillman, 1960; Tapinocalymene gen. nov. (herein; see Chapter F).

DIAGNOSIS. Glabella bell-shaped; it has three or four lateral glabellar lobes which are well inflated and lateral glabellar furrows which are distinct. Facial sutures gonotoparian. No preglabellar field. Papillate-buttress structure present. No ala or crescentic area outside lateral glabellar lobe 1p. Hypostome with discrete raised area or protuberance on anterior lobe. Genal spines absent.

DISCUSSION. The Calymeninae is here limited to contain only those (morphologically 'advanced') genera that have the axial furrow bridged by a genal buttress which is in contact with a lateral glabellar lobe. Following the present investigation, all known hypostomes of the members of this subfamily (Calymene, Diacalymene, Papillicalymene, Spathacalymene, and Tapinocalymene) have some form of raised area or protuberance on the anterior lobe - an additional feature which helps distinguish them from other genera previously regarded as calymenines (cf. diagnosis of Flexicalymeninae subfam. nov. in Chapter B). I am in agreement with the view (Shirley 1936; Whittington 1971) that members of the Calymeninae (as here restricted) represent a major evolutionary stock.

Genus Diacalymene Kegel, 1927

TYPE SPECIES. Calymene diademata Beyrich, 1846, p. 24, pl. 2, figs. 4a, c; from the Liten Formation (Wenlock), Svaty Jan, Bohemia. By original designation of Kegel, 1927, p. 617.

OTHER SPECIES. D. allportiana (Salter, 1865); D. asperula (Vanek, 1965); D. consimilis (Cooper, 1930); D. crassa Shirley, 1936; D. drummuckensis (Reed, 1906); D. gibberosa sp. nov.; D. marginata Shirley, 1936; D. schucherti Twenhofel, 1928; D. vogdesi (Foerste, 1887). Diacalymene ? rhenana Kegel, 1927.

DIAGNOSIS. Glabella parabolic to bell-shaped in outline. The boundary between the preglabellar furrow and anterior border is marked by a ridge or sharp change in slope. Genal buttress is in contact with papillate lateral glabellar lobe 2p. Hypostome has small protuberance on anterior lobe of median body. Inner anterior corner of fixed cheek typically projects forwards and inwards towards anterior border. Glabellar tubercles characteristically fine and closely set.

DISCUSSION. Shirley emended Kegel's concept of Diacalymene and differentiated it from Calymene on the presence of a 'ridge' which occurs between the preglabellar furrow and anterior border. In my experience the strength of this 'ridge' shows some variation both between, and within species assigned to Diacalymene. In cases where this 'ridge' is less distinctly developed, it may be more appropriate to describe the boundary between the anterior border and preglabellar furrow as simply a change of slope. Within a single specimen, the ridge or change of slope is invariably better defined opposite the lateral margin of the glabella than on the median line. Furthermore, if the true nature of the ridge is to be determined, it is essential that only those specimens with the cuticle extant (or casts of external moulds) should be taken into consideration.

Diacalymene is obviously closely related to Calymene and no doubt gave rise to that genus (Whittington 1971, p. 457). It is argueable whether Diacalymene is worthy of generic recognition. However in the author's opinion, the feature on which Shirley's concept of Diacalymene is based can be recognised in a number of species and unites a group of related Upper Ordovician and Silurian taxa which are worthy of generic distinction from Calymene (s.s.). Certainly D. diademata, the species which displays the most strongly developed ridge, should not be considered congeneric with C. blumenbachii.

Other characters which in the majority of cases aid in the differentiation of Diacalymene from Calymene include the forward and inwardly projecting anterior corner to the fixed cheek, the less strongly developed protuberance on the hypostome, and the very fine, closely set, glabellar tubercles.

Within the Diacalymene species I have studied two informal groupings are discernible (cf. Shirley 1936, p. 415), based on the form of the glabella. The first group has a more bluntly developed outline to the frontal glabellar lobe and often has more subquadrate 1p and 2p lateral lobes; it includes D. diademata, D. drummuckensis, D. consimilis, D. allportiana and probably D. asperula. The second group typically has a much more rounded frontal glabellar lobe, a glabellar outline which is often more subparabolic and subcircular lateral glabellar lobes; it includes D. crassa, D. vogdesi, and D. gibberosa. The second group is considered to be an offshoot from the main Diacalymene stock which includes drummuckensis and diademata.

Diacalymene, and indeed the Calymeninae, may have arisen from Gravicalymene Shirley, 1936, species of which are contemporareous with Kegel's genus in strata of Ashgill age.

OCCURRENCE. As here defined the world-wide stratigraphical range of Diacalymene is from the Ashgill to the Wenlock.

In N America the genus is represented by three established species (D. consimilis; D. vogdesi; D. schucherti) from strata of Ashgill to Llandovery age. Lesperance (1970, p. 1880, fig. 6) has indicated the presence of a Diacalymene species in the Pridolian of Quebec; this species awaits description.

In Europe the genus has been documented from Britain, Scandinavia and Bohemia; in all three areas the range of Diacalymene is Ashgill to Wenlock. D. marginata from the Pusgillian of Britain represent the earliest member of the genus.

D. marginata (Shirley, 1936)

Plate 1, figs. 1-11; Plate 2, figs. 1-4, 6, 7, 9-11.

1935 Calymene aff. drummuckensis; Lamont, pp. 297, 298.

1935 Calymene sp.; Lamont p. 298.

1936 Diacalymene marginata; Shirley, p. 415, pl. 29, figs. 19, 20.

1938 Diacalymene drummuckensis; Whittington, p.

1945 Reacalymene (?) holtedahli n. sp.; Stormer, p. 415, pl. 2, figs. 6-8.

1949 Diacalymene marginata; Bancroft, p. 309.

1965 Diacalymene marginata Shirley; Cave, p. 295.

? 1965 Diacalymene marginata; Cave, p. 296.

1966 Diacalymene marginata Shirley; Ingham, p. 486.

1966 Diacalymene marginata Shirley; Whittington, p. 123.

1970 Diacalymene marginata Shirley; Ingham, p. 17.

HOLOTYPE. Incomplete internal mould cranidium; Begg Collection BG 1010; figured Shirley 1936, pl. 29, fig. 19. This cranidium is believed to be lost. The following information was obtained from the catalogue card for this specimen - which should have been housed at the Hunterian Museum, Glasgow; "This specimen was returned by Dr. Shirley to Mr. Begg through Dr. Lamont. Neither Mr. Begg nor Dr. Lamont can explain its absence. 28. 10. 41". Dr. J.K. Ingham (pers. comm.) is proposing to erect a neotype for the species in the second part of his monograph on the Ashgill trilobites from the Cautley and Dent, districts of northern England. This cranidium is figured here on Pl. 2, figs. 7, 10, 11.

TYPE STRATUM AND TYPE LOCALITY. Lower Drummuck Group, Ashgill Series, 680 yards SW of High Mains Farm, Quarrel Hill, near New Dailly, Girvan district, Ayrshire. This corresponds to locality 3 of Lamont (1935, p. 300, pl. 9). Ingham (1966, p. 488) correlated the Lower

Drummuck Group of the Girvan district with Zone 1 of the Cautleyan Stage, Ashgill Series.

DISCUSSION. The holotype of this species is reported lost (see above). As far as I am aware only one other topotype specimen is available for study, and this is figured here on Pl. 2, figs. 7, 10, 11. Shirley differentiated marginata by its moderately upturned anterior border and the "three slight convexities" on the ridge of the preglabella area. The so-called convexity opposite each axial furrow is present in all species of Diacalymene. The convexity which lies opposite the frontal glabellar lobe is well seen on the holotype (Shirley 1936, pl. 29, fig. 19), but is much weaker on the available topotype specimen.

In the original description several specimens of middle Ashgill age from a number of dispersed British localities were referred to marginata; differences can be observed between some of these specimens. For example in the only two specimens I have from the Lower Drummuck Group the topotype cranidium has a relatively narrower anterior border and a more sharply projecting anterior corner to the fixed cheek (cf. Pl. 2, figs. 3, 11). Similarly the cranidium (Pl. 2, fig. 6) cited by Shirley from N Wales, differs both from other Welsh cranidia (Pl. 2, figs. 1, 2.) and from the Scottish material by its much longer preglabellar furrow. Some of these differences may be due to aspects of preservation (particularly the cranidium on Pl. 2, fig. 6), while other differences may hold taxonomic significance.

Until more sufficiently well preserved topotype cranidia become available for study I prefer to place all this material under the name marginata. The confines of this species as used herein is necessarily broad, but on the best preserved external mould cranidium I have examined (Pl. 2, fig. 1), the species seems to be largely characterized by its long, narrow glabella and fairly long, moderately upturned anterior border. With the aid of Ingham's N England material (to be published) it may yet be possible to more adequately diagnose this species from outside the type area.

Reacalymene ? holtedahli Størmer, 1945 was erected on the basis of material from the Tretaspis Shale of the Hadeland district, Norway. An attempt by the present author to collect topotype material of this taxon, which can be referred to Diacalymene, met with no success. The best preserved extant material (figured here Pl. 1, fig. 1) shows no serviceable difference from British specimens of marginata (cf. Pl. 1, fig. 1 with Pl. 2, fig. 2)

OCCURRENCE Lower Drummuck Group, Girvan area. Upper Pusgillian and Zones 1 and 2 of the Cautleyan, Cautley and Dent districts of Westmorland and Yorkshire (Ingham 1966, p. 486). Applethwaite Beds (Cautleyan Zones 2 and 3), Kentmere district (Ingham 1966, p. 489). Lower Trewylan Beds, Montgomeryshire (Ingham 1966, p. 494). Ddolhir Beds, N Wales. Tretaspis Shale, Norway. Slade Beds, Pembrokeshire? (Cave 1965, p. 296). Pusgillian of the Cross-Fell Inlier? (Dean 1962, p. 116).

Diacalymene sp. indet.

Plate 1, fig. 9

MATERIAL Internal mould of incomplete cranidium, PMO 91114; coll. J.F. Bockelie 1964.

OCCURRENCE. Stage 5a (= upper Ashgill), Øvre Nes badestrand, Asker district, Oslo Region, Norway.

DISCUSSION This single cranidium is too ill preserved to allow a specific assignment, but can be referred to Diacalymene. It represents the last occurrence of the genus in the Ordovician of Norway.

Diacalymene drummuckensis (Reed, 1906)

Plate 4, figs. 1-11; Plate 5, figs. 1-12; Plate 6, figs. 4, 8, 9.

1851 Calymene Blumenbachi , Brongn.; Salter in Murchison, p. 177, pl. 9, figs. 1a, b.

1851 Calymene Blumenbachii (Brong.); McCoy (pars) in Sedgwick & McCoy, p. 165

1865 Calymene Blumenbachii, Brongn, var. a, auctorum; Salter, pl. 8, fig. 9, pl. 9, fig. 2a, ? fig. 2b, non figs. 1a, b.

1866 Calymene Blumenbachii; Salter, pl. 17, figs. 1, 2.

1873 Calymene Blumenbachii, Brongn.; Salter (pars), p. 77.

1879 Calymene Blumenbachii, Brongniart.; Nicholson & Etheridge, p. 140, pl. 10, figs. 2-5, non fig. 6.

1906 Calymene blumenbachii, auct., var. nov. drummuckensis; Reed, p. 135, pl. 17, fig. 14, pl. 18, figs. 1-4.

1931 Calymene drummuckensis Reed, 1906; Shirley, p. 28, pl. 2, figs. 7, 8.

1931 Calymene blumenbachi Brongniart (= tuberculata (Brunnich)), var. drummuckensis, Reed; Reed, p. 21.

1935 Calymene drummuckensis; Lamont (pars), pp. 297, 298.

1936 Diacalymene drummuckensis; Shirley, pp. 416, 417.

1943 Calymene drummuckensis (Reed); Begg, p. 62, pl. 2, fig. 3.

1949 Diacalymene drummuckensis (Reed); Bancroft, p. 309.

? 1966 Diacalymene drummuckensis (Reed); Ingham, p. 486.

LECTOTYPE. Selected herein; incomplete cranidium with cuticle partially remaining; BM In 23370; Gray Collection; figured Nicholson & Etheridge 1879, pl. 10, fig. 4, 4a, also Reed 1906, pl. 18, fig. 3, also herein Pl. 4, figs. 8, 9, 11.

TYPE STRATUM AND TYPE LOCALITY. Upper Drummuck Group, Rawtheyan Stage, Ashgill Series, Drummuck, near Girvan, Ayrshire, Scotland.

PARALECTOTYPES. Internal mould of hypostome and counterpart, BM In 23381, figured Reed 1906, pl. 17, fig. 14; internal mould of incomplete cranidium, BM In 23382, figured Reed 1906, pl. 18, fig. 1; internal mould of nearly complete individual, BM In 23380, figured Reed 1906, pl. 18, fig. 2; complete pygidium, BM In23383, figured Reed 1906, pl. 18, fig. 4; internal mould of nearly complete individual, BM In 23368, figured Nicholson & Etheridge 1879, pl. 10, fig. 2; internal mould of thorax and pygidium, BM In 23369, figured Nicholson & Etheridge 1879, pl. 10, fig. 3; internal mould of pygidium, BM In 23371, figured Nicholson & Etheridge 1879, pl. 10, fig. 5.

ADDITIONAL MATERIAL. Numerous (more than fifty) specimens of cranidia and pygidia, nearly all of which are internal moulds though some still have part of the cuticle extant. Disarticulated thoracic segments are common, entire individuals rare. All of the major British Museums have material of this species, especially the British Museum (Natural History) and Hunterian Museum, Glasgow.

DIAGNOSIS Glabella weakly bell-shaped in outline, tapers gradually anteriorly. Preglabellar furrow very narrow and deep, anterior border quite short (sag.), moderately to fairly strongly inclined. Dorsal and outer sides of anterior border are about equal in width, make a right-angle outline in lateral profile. U-shaped lateral border furrow. Six pygidial axial rings, five pleural furrows.

DESCRIPTION. Glabella longer than wide, bell-shaped in outline, stands proud above fixed cheek. Occipital ring widest medially. Occipital furrow quite deep and narrow (sag.) behind central glabellar area, more so behind lobe 1p, on internal moulds considerably broader. Basal glabellar lobe is large, quite strongly inflated, varies from subquadrate to subcircular in outline, separated from central area of glabella by shallow depression. Lateral furrow 1p very deep at axial furrow, extremely narrow as it passes inwards and backwards between lobes

1p and 2p, is directed more posteriorly around inner margin of lobe 1p, shallows abruptly at inner 'neck' of this lobe; a shorter, very much weaker anterior branch of 1p furrow runs forward around inner side of lobe 2p; no intermediate lobe. Lobe 2p mid-way in size between 1p and 3p, subquadrate to subcircular in outline, blunt abaxial margin in contact with very short (tr.), weakly projecting genal buttress. Furrow 2p deeply incised, directed transversely or somewhat backwards, joins anterior branch of furrow 1p. Lobe 3p distinct, strongly inflated, subcircular or transversely elongate in dorsal view, sited on dorsolateral glabellar margin. Furrow 3p sharply impressed. Some specimens show faint swelling in front of lobe 3p suggesting a fourth lobe; no 4p furrow. Subrectangular frontal glabellar lobe about three and a half times as wide as long, sides exsagittally directed or trend gently inwards, anterior margin bluntly rounded, falls vertically and slightly overhangs preglabellar furrow, juts in front of fixed cheek. Central area of glabella narrows towards occipital furrow.

Axial furrow deep and exceedingly narrow beside lobe 1p, runs under bridge of lobe 2p and genal buttress, widens (tr.) only fractionally in front of lobe 2p, maintains near constant depth until coalescing with preglabellar furrow. Anterior pit situated in base of furrow below side of frontal lobe.

Preglabellar furrow very narrow (sag. & exs.), rather deep and trench-like, widens slightly abaxially near axial furrow. Junction of vertically inclined anterior wall of preglabellar furrow and posterior margin of moderate to steeply inclined dorsal surface of anterior border is ridge-like; this ridge best developed opposite lateral margin of frontal glabellar lobe where anterior border is slightly wider (exs.). In lateral profile dorsal surface of anterior border is flat or gently convex, turns quite sharply over at anterior edge to run into its outer side which swings downward and fractionally forward in a broad ar to rostral suture; dorsal surface and outer side of anterior border are about equally wide. Anterior margin (dorsal view) usually gently convex forwards.

Posterior margin runs transversely from axial furrow, bends posteriorly at fulcrum, swings forwards near genal angle. Posterior border furrow widest (exs.) one third of its length from axial furrow to facial suture. Inner, anterior corner of fixed cheek projects somewhat forward and inward toward slight swelling on anterior border. Palpebral lobe centred opposite middle of lateral glabellar lobe 2p, about as long as that lobe, inclined upwards at low angle; palpebral lobes relatively near axial furrow, are from 1.4 to 1.9 times as wide apart as width across glabella at lobes 2p. Adaxially from eye lobe fixed cheek is gently convex upwards, about horizontal in attitude to genal buttress. Posterior branch of facial suture directed firstly outwards from eye lobe, swings backwards towards lateral border furrow where it turns sharply more backwards before finally bending outwards to bisect lateral and posterior margins. Anterior branch runs forward to anterior margin, turns abruptly inward and downward across outer side of anterior border to meet rostral suture.

Free cheek bears narrow eye socle, inner part slopes steeply to deep, U-shaped lateral border furrow. Lateral border widest posteriorly, convex, curves over and under to join acutely reflexed doublure which projects upward, and outward. Rostral suture broadly arched; connective suture directed inward, downward, backward; inner arc of border sector subparallel with rostral suture for most of its length (tr.) but approaching connective suture flexes sharply backwards, this flexure also present on doublure sector.

Anterior border of hypostome ventrally directed; anterior wing with a deep pit. Between anterior and posterior wings, embayment of lateral margin is abaxially convex. Lateral border narrowest near posterior wing, expands posteriorly into flat-topped, broad-based spine, near anterior wing is roll-like in section (tr.). Lateral border furrow shallowest mid-way between wings; posterior border furrow a short (tr.), sharp nick. Median body weakly divided by very faint median furrow which connects two weakly inflated, oval maculae. In the centre of anterior lobe is a short, subcircular protuberance. Crescent shaped posterior lobe falls quite steeply to lateral and posterior border furrows.

Thorax composed of thirteen segments. I have not seen any well preserved external moulds, the cast of a squashed specimen (BM In 43025; Pl. 5, fig. 7) has weakly arched axial ring and articulating half-ring (sag.), gentle distal inflation of axial ring, and well-incised U-shaped pleural furrow. Pleural doublure curves around abaxial margin of pleuron, progressing upwards on anterior side to form a stop to enrollment.

Pygidium is described from paralectotype (Pl. 5, figs. 8, 11, 12). It is about 1.3 times as wide as long; axis is about 0.4 times as wide as pygidium, six axial rings - five of them complete, anterior two rings with very faint distal inflation. Ring furrows best marked near axial furrow, become progressively weaker posteriorly, first five are complete, sixth effaced medially. Distinct terminal axial piece has bluntly rounded outline, falls vertically to postaxial sector. Axial furrow clearly marked throughout its length except behind central portion of terminal axial piece. Pleural region slopes downwards more steeply distally than proximally; five well marked pleural furrows just fail to reach lateral margin. Inner half of first four pleural furrows extremely faint, outer half clearly incised, marginally longer than pleural furrows. Fifth interpleural forms side of postaxial sector.

Ornament on cranidium and inner part of free cheek consists of closely-spaced, small, rounded tubercles and granules (Pl. 4, fig. 11). On ventral facing slope of lateral border tubercles become more flattened and scale-like; those on border sector of rostral plate also flat-topped but have circular outline - not so elongate as on border roll. On border sector of rostral plate adjacent to inner arc the granules are very small and appear to be arranged in two rows parallel to this arc. Ornament on hypostome not well preserved, scattered granules observed over much of surface especially lateral borders and posterior spines. Thorax has same type of tubercles as cranidium.

DISCUSSION. Abundant material of this species is available but rarely is the fossil found with the cuticle remaining. All cranidia previously illustrated have been internal moulds or near internal moulds. Material is figured here which gives a clearer picture of much of the external morphology of the species; in particular the true form of the preglabellar area is well shown by at least two of the specimens (WM unnumbered and RSM 1968. 50. 34A). Many of the internal moulds examined (including the lectotype) display little of the quite strong break in slope separating the preglabellar furrow from the anterior border. No evidence has been found to support the claim (Reed 1906, p. 135) that drummuckensis possessed a a median occipital tubercle.

From an unusually well preserved external mould (Pl. 6, figs. 7, 8) one can see both rostral plate and hypostome in their original positions. The inner arc of the doublure sector of the hypostome does not completely parallel the rostral suture but near the connective suture flexes sharply backwards. This flexure is reflected onto the doublure sector and allows the abaxial margins of this sector to fit inside the anterior wings of the hypostome. The outline of the inner arc also reflects that of the postaxial sector of the pygidium. Thus during enrollment the central and abaxial parts of the inner arc would fit tightly against the steep posterior and lateral margins of the pygidial postaxial sector. This type of outline to the inner arc of the rostral plate is also present in D. aff. drummuckensis and Diacalymene sp. A which are described below, and certain species of Calymene (see C. neointermedia, Chapter E), but has not yet been recorded in genera of the Flexicalymeninae (as conceived herein).

D. drummuckensis is the earliest species so far recorded with a median protuberance on the anterior lobe of the hypostome. Inmost Silurian species of Calymene this feature has evolved into a more conspicuous spine-like structure. The hypostome of D. diademata from the Wenlock of Bohemia is like that of drummuckensis in possessing a comparatively small protuberance, but seems to be somewhat wider than in the Ordovician species.

A comparison of D. drummuckensis with diademata and D. consimilis (Cooper, 1930) is given below.

D. marginata appears to differ from drummuckensis in its relatively narrower glabella, longer anterior border, and having a more strongly developed ridge between the preglabellar furrow and anterior border.

OCCURRENCE Apart from the upper Drummuck Group of the Girvan area Lamont (1935, p. 298) also records drummuckensis from the lower Drummuck Group of this district. Ingham (1966, p. 486, table 2) has recorded, but not yet described, drummuckensis from the Cystoid Limestone (= topmost Rawtheyan Stage, see Ingham and Wright in Williams et al. 1972, p. 48) of the Murthwaite and Taythes Inliers of northern England.

Diacalymene aff. D. drummuckensis (Reed, 1906)
Plate 7, figs. 1, 4, 8; Plate 8, figs. 1-4, 6-8.

MATERIAL AND OCCURRENCE. All the material is from the Dalmanitina Beds (= upper Ashgill) of Sweden.

The following are from Borenshult, Östergotland: One incomplete cephalon, RM Ar18581; seven incomplete, partially exfoliated cranidia, RM Ar 18561-563, RM Ar18569-570, RM Ar18576-577; two incomplete internal mould cranidia RM Ar18591, RM Ar18591; seven incomplete pygidia, mostly or partially exfoliated, RM Ar17763, RM Ar18571-575, RM Ar18583;

five incomplete external mould pygidia, RM Ar18585-588, RM Ar18590; two incomplete external mould pygidia RM Ar18582-Ar18584.

The following internal mould cranidia are from Alleberg, Vastergotland: RM Ar14993, RM Ar14978, RM Ar14996, RM Ar15080, RM Ar15112, RM Ar15140, RM Ar15176, RM Ar15203, RM Ar15205, RM Ar15224, RM Ar47703.

DISCUSSION . In the Riksmuseum there are several calymenid specimens from the Upper Ordovician of Borenshult, Östergotland, which form part of Lindström's collections. Some of the material is in internal mould form and all of it is incomplete except for one excellently preserved cephalon (RM Ar18581) which can be referred to Diacalymene. The Borenshult Diacalymene is allied to D. drummuckensis (Reed) though it can be discriminated by its shallower preglabellar furrow, more horizontally projecting anterior border, relatively narrower outer side to the anterior border, unusually wide lateral border furrow on the free cheek, and possibly a more sharply tapering pygidial axis. These differences are sufficient to enable specific separation of the Borenshult material from drummuckensis but problems arise when attempting a comparison of the Swedish species with D. consimilis and D. asperula, both of which seem closely related but are inadequately known.

This group of Ashgill species are all very similar. At present we have a much greater knowledge of Reed's Scottish species than consimilis or asperula. Until the Quebec and Bohemian taxa are known in as much detail, and redescribed with the aid of sufficient, well preserved material, the Borenshult species can only be distinguished with certainty from drummuckensis, and the establishment of a new species here would be premature. From the material at hand the two cranidia of consimilis (see description below) show more sharply convergent axial furrows on the cranidium than the Swedish species.

There is a species of Diacalymene which is reasonably abundant in the Dalmanitina beds at Alleberg, Vastergotland, but the specimens are internal moulds and most of them are slightly flattened. In some specimens the dorsal surface of the anterior border is fractionally more inclined than in the Borenshult cranidium, but I have otherwise found difficulty in being able to separate the two and have provisionally regarded them as one species. It is interesting to note that the Alleberg material is associated with a Flexicalymene species which is very close to, if not conspecific with, F. incerta (Barrande, 1846) from the Zahorany and Dohdalec Formations in Bohemia. The Vastergotland cranidium is very close to D. asperula from Bohemia but on the evidence from internal moulds differs mainly in having the ridge between anterior border and preglabellar furrow more sharply defined. It also differs from D. drummuckensis in this respect, together with its shallower preglabellar furrow.

This represents the first record of Diacalymene from Sweden.

Diacalymene consimilis (Cooper, 1930)

Plate 6, figs. 1-3, 5, 6.

1930 Calymene consimilis Cooper, n. sp.; Cooper in Schuchert & Cooper, p. 385, pl. 5, figs. 24, 25.

1968 Diacalymene consimilis Cooper; Lesperance, p. 148, table 1.

HOLOTYPE. Incomplete cephalon with seven thoracic segments; Cat. No. 12887 P.M.; figured Cooper in Schuchert & Cooper 1930, pl. 5, fig. 24.

TYPE STRATUM AND TYPE LOCALITY. White Head Formation, Upper Ordovician, locality F_8 of Schuchert & Cooper (1930; see p. 162, fig. 1), South Cove, Perce area, Quebec. Lesperance (1968) regarded that part of the White Head Formation containing D. consimilis to be of lower or middle Ashgill age.

PARATYPE. Small pygidium; Cat. No. 12886 P.M.; figured Cooper in Schuchert & Cooper 1930, pl. 5, fig. 5.; from the White Head Formation, Priests Road, Perce area, Quebec.

MATERIAL. Incomplete cranidium, DM It7392; incomplete cephalon with several thoracic segments, DM It7393.

DESCRIPTION. Glabella bell-shaped in outline. 1p lateral lobe just less than one third as wide as glabella, subquadrate in outline with outer margin strongly convex abaxially, semi-isolated from central area by shallow depression across inner 'neck'. Furrow 1p very deep and narrow between lobes 1p and 2p, then bifurcates, posterior branch considerably deeper and longer than very much weaker, shallow anterior branch. No intermediate lobe. Subcircular to subquadrate lobe 2p joined to genal buttress. Furrow 2p deep and distinct. Conspicuous lateral lobe 3p transversely elongate, defined anteriorly by well marked furrow 3p. Very small lobe 4p present on one of the specimens (DM It 7392). Frontal lobe very short (sag. & exs.), just over half as wide (tr.) as glabella at lobes 1p. Anterior margin broadly arcuate in outline - descends steeply to preglabellar furrow, protrudes just in front of fixed cheek.

Axial furrow very narrow and deep around lobe 1p, only fractionally wider at furrow 1p and anterior to lobe 2p. Preglabellar furrow a fairly deep, narrow channel, posterior side undercuts frontal lobe, anterior side slopes vertically to meet posterior margin of moderately inclined anterior border. Dorsal side of the latter maintains constant width to axial furrow, narrows from here to facial suture.

Palpebral lobe centred opposite middle of lateral lobe 2p. Anterior adaxial corner of fixed cheek somewhat inflated, points inward and forward. Anterior branch of facial suture directed forward and inward to anterior margin, turns sharply inward across anterior facing slope of anterior border to run to rostral suture.

On the more complete cranidium (BM It 7392) much of surface ornamentation obliterated, but what little remains and on other cranidium (BM It 7393), consists of very fine, closely-spaced tubercles and granules.

DISCUSSION. This Upper Ordovician species from Quebec is in need of a full revision. Such a study lies outside the scope of the present work but D. consimilis is so closely related to some of the species discussed herein that the opportunity was taken to figure and comment on two specimens (from the Brit. Mus. Nat. Hist. collections) which are assigned to the Quebec taxon. Both specimens are from the White Head Formation, Mont Joli, Perce, Quebec. South Cove, the type locality for consimilis, is on the southern side of Mont Joli (see Schuchert and Cooper 1930, p. 162, fig. 1).

Cooper figured two specimens of his new species, one (pl. 5, fig. 25), a paratype pygidium, the other (pl. 5, fig. 24), the holotype which is an incomplete cephalon with seven attached thoracic segments. From his illustrations of the holotype and the two specimens I have available there can be no doubt that consimilis belongs in Diacalymene and that it is very close to D. drumuckensis (Reed, 1906). The affinities of the Upper Ordovician Perce faunas with those of N Europe was noted by Schuchert (in Schuchert and Cooper 1930, p. 161) and in particular Lesperance (1968, p. 149, table 1) has suggested that the lower or middle Ashgill Stenopareia fauna of the Perce Region, in which D. consimilis occurs, is closely allied to that of the Drummuck Group of the Girvan area. This is substantiated here with regard to the calymenids. The shape of the lateral glabellar lobes, bluntly rounded frontal glabellar lobe, nature of the axial and preglabellar furrows, general form of the anterior border, finely tuberculate ornament and number of axial rings and pleural furrows on the pygidium are alike in consimilis and drummuckensis. Two characters appear to stand in favour of separating the North American, from Scottish species: in the former the glabella seems relatively wider across lateral lobe 1p compared with its width across the frontal glabellar lobe, and the dorsal surface of the glabella does not project quite so dominantly above the fixed cheeks.

Lesperance (1968, p. 150, table 2, p. 156, table 6) has also recorded Diacalymene sp. aff. consimilis from the lower or middle Ashgill Hemipyga fauna and the Llandoverian (undifferentiated) part of the White Head Formation, Perce Region, but this species awaits description. Calymene schucherti Twenhofel from the Jupiter Formation (= middle to late Llandovery in age; Bolton 1972, p. 16) of Anticosti Island has not been discussed since it was erected in 1928, but Bolton (1972, pl. 9, figs. 3, 9, pl. 10, figs. 12, 17) has recently provided good illustrations of the species and referred it to Diacalymene. D. schucherti (Twenhofel, 1928) appears to differ from D. consimilis through its more rounded frontal glabellar lobe, wider (sag.) preglabellar furrow, much narrower (tr.) central glabellar area between the very wide 1p glabellar lobes, the possession of an intermediate lobe on the side of the glabella within the adaxial fork of 1p furrow, and eight axial rings on the pygidium (see also Twenhofel 1928, pl. 5, fig. 1). However, like D. consimilis, D. schucherti seems to have a relatively wide glabella at lobes 1p which then narrows quite strongly (extremely in the case of GSC No. 29695, Bolton 1972, pl. 9, fig. 3) anteriorly. The consimilis stock may have given rise to schucherti.

OCCURRENCE. Ashgill part of the White Head Formation, Quebec.

Diacalymene asperula (Vanek, 1965)

Plate 7, figs. 2, 3, 5-7, 9, 10.

1872 Calym. Blumenbachi Brongn.; Barrande, p. 36, pl. 14, fig. 33.

1958 Diacalymene asperula sp. n. (nom. nud.); Vanek, p. 113.

1965 Gravicalymene asperula sp. n. Vanek, p. 21, pl. 1, figs. 1, 2, p. 23, text-fig. 1.

1966 Gravicalymene asperula; Havlicek & Vanek, p. 41.

1970 Gravicalymene asperula Vanek; Vanek in Horny & Bastl, p. 75.

HOLOTYPE. Internal mould of incomplete cranidium; UUG, JV 1643; figured Vanek 1965, pl. 1, fig. 1.

TYPE STRATUM AND TYPE LOCALITY. Highest part of the Kraluv Dvur Formation, Ordovician, Kosov near Beroun, Bohemia. Williams (in Williams, Strachan, Bassett, Dean et al. 1972, fig. 2) correlates the Kraluv Dvur Formation with the whole of the Cautleyan and Rawtheyan of the Ashgill Series.

PARATYPE. Distorted pygidium, JV- 1642. From type stratum and type locality.

MATERIAL. I have only three specimens available of this species (L Mk 1-3), all are internal mould cranidia and one of them (L Mk 3) has an external mould counterpart. The material was kindly loaned by Dr. L. Marek.

DESCRIPTION. Glabella longer than wide, weakly to moderately bell-shaped in outline. Occipital furrow considerably deeper behind lateral lobe 1p than median glabellar lobe. Lobe 1p about one third as wide as glabella, subquadrate to subovoid in outline. Deep lateral furrow 1p curves inward and backward; very shallow anterior branch runs inward and forward over adaxial side of subcircular or slightly elongate (tr.)

lobe 2p. No intermediate lobe in fork of furrow 1p. Lateral furrow 2p transversely directed. Small lobe 3p perched on dorsolateral glabellar surface. Suggestion of very weakly inflated lobe 4p. Frontal glabellar lobe projects in front of fixed cheek, is gently arched forwards in outline, falls steeply to preglabellar furrow.

Axial furrow extremely narrow around lateral lobe 1p, widens slightly at furrow 1p, is constricted in depth opposite furrow 2p, is rille-like with steep outer slope at side of lobe 3p and frontal lobe, noticeably expands only when reaching preglabellar furrow. Latter is narrow (sag. & exs.), moderately deep with steep anterior face. On internal moulds dorsal surface of anterior border is gently convex (sag.), flatter on a cast of one external mould (Pl. 7, fig. 5), posterior margin swollen opposite axial furrow.

In internal moulds boundary between preglabellar furrow and anterior border marked by break of slope, in external mould this boundary more ridge-like. Outer side of anterior border is mildly convex (sag.), runs downward and slightly forward to a very broadly arched rostral suture. Anterior margin broadly arcuate. Rostral plate and hypostome unknown.

In lateral profile posterior part of fixed cheek is about horizontally inclined between palpebral lobe and posterior border furrow; in front of eye lobe it slopes gently downwards. Palpebral lobe sited opposite lateral lobe 2p. Inner, anterior corner of fixed cheek may be a little pointed and inflated but does not overhang furrow. Weakly projecting genal buttress reaches from fixed cheek towards lateral lobe 2p.

Axis of pygidium narrows quite sharply posteriorly, contains five to six axial rings and terminal axial piece. Pleural region has five pleural and interpleural furrows, the latter are deeper distally than proximally. Surface of glabella and pygidium (excluding all furrows), covered with fine, closely-set granules. (Description of pygidium and ornamentation taken from Vanek 1965, p. 23 and pl. 1, fig. 2).

DISCUSSION. Novak's manuscript name, Calymene asperula, was made available by Vanek (1965) who referred the species to Gravicalymene. The need for better illustration of this species is only partly fulfilled in the present account. My observations on asperula are largely based on three cranidia which, I am assured (Dr. L. Marek pers. comm.), are topotype specimens.

The true form of the anterior border is not represented in these internal mould specimens but fortunately one of them (Pl. 7, fig. 5) has a counterpart external mould which shows it to be of the Diacalymene or Gravicalymene type. The presence of a genal buttress connected to glabellar lobe 2p would be diagnostic of Diacalymene. Vanek (1965) does not mention such a structure in his description and none can be discerned from his photograph (1965, pl. 1, fig. 1) of the holotype but this specimen is an internal mould and is therefore not likely to have the lobe in contact with the fixed cheek. In Marek's specimens the buttress is present, but not immediately obvious. This inconspicuousness is in part due to the internal mould condition of the cranidia, but largely because of the narrow axial furrow. Thus asperula is here transferred from Gravicalymene to Diacalymene. As far as can be determined D. asperula is similar to other species of Diacalymene of approximately upper Ashgill age and it is difficult on the basis of internal mould material to discriminate between them. Extra topotype external mould material is required to enable an adequate diagnosis of the Bohemian species and to facilitate a more accurate comparison with other taxa. Vanek (1965, p. 23, text-fig. 1) depicts asperula as having a medially pointed anterior margin. If this were so it would immediately distinguish the species from all other members of Diacalymene, but in the specimens figured here, the anterior margin is gently curved and it is suggested that Vanek's illustration may have been based on a distorted cranidium. Also I have seen no indication of what that author termed a "faintly distinct pair of nipple-like nodes" at the adaxial side of lateral furrow 1p, or a median tubercle on the occipital ring. D. asperula is of about the same age as D. drummuckensis and as far as the present material is concerned appears to differ morphologically through its slightly shallower preglabellar furrow and less projecting anterior corner to the fixed cheek. The anterior border in internal moulds of asperula and drummuckensis is not disimilar (compare Pl. 7, fig. 3 with Pl. 4, fig. 9); in external moulds that of asperula seems to be less steeply inclined but this specimen(Pl. 7, fig. 5) has been somewhat flattened. D. asperula may eventually prove to be a junior synonym of drummuckensis.

OCCURRENCE. Only recorded from the Kraluv Dvur Formation where it is confined to the uppermost layers (= upper Rawtheyan) and associated with Cryptolithus kosoviensis. In addition to the type locality Vanek (1965, p. 24) also records the species from Zadni Trebau, Liten and Praha-Nusle.

Diacalymene sp. A

Plate 9, figs. 3, 7-9; Plate 8, fig. 5.

MATERIAL. One cranidium, IPU Ar1778.

OCCURRENCE. Djupvik, Eksta, Gotland.

DISCUSSION. In the display collections of the Palaeontological Institute of Uppsala Museum there is a large cranidium of a Diacalymene species which is labelled as coming from Djupvik, Eksta. This is a Gotland locality and the deposits here are the Mudle Beds which are Upper Wenlock in age. Assuming the locality information to be correct, this specimen is the only Diacalymene I have seen from the Silurian of Gotland.

Its affinities lie more with Upper Ordovician, than Silurian species. It is especially like the Östergotland material that was described above as Diacalymene aff. D. drummuckensis. In particular it has the same type of preglabellar area and lateral border furrow that is found in, and was used to distinguish, the Borenshult species. Also the rostral plates of the Gotland and Östergotland cranidia both show a posteriorly directed flexure on the inner arc of the border sector (Pl. 8, fig. 5).

Apart from some differences which are probably a result of its greater size - for example more swollen basal glabellar lobes in the Silurian specimens - the only marked difference I can discern between the Borenshult and Gotland cranidia is the relatively much smaller 3p glabellar lobe in the latter. The significance of this is difficult to assess in the absence of a larger sample from the Wenlock horizon. The Borenshult and Gotland cranidia are unquestionably closely related; I hesitate to assign them to the same species on account of the difference in the 3p lobe and the considerable time gap separating the two.

Diacalymene sp. B.

Plate 2, figs. 5, 8; Plate 3, figs. 1-7.

1908 Calymene trinucleina LNS MSCR.; Wiman, p. 135, pl. 8, figs. 28-32.

MATERIAL. Two almost complete individuals, RM Ar47706, SGU unnumbered.

OCCURRENCE. RM Ar47706 is from the Dalmanitina Beds, Kullsberg, Dalarna, Sweden; the SGU specimen is from an erratic of the Östersjö Limestone (= Jerrestadian in age - see Jaanusson 1963, pp. 138, 139) from the N Baltic, coll. Schmalensee, 1886.

DISCUSSION. These two almost complete individuals are alike and differ from other established species in the relative shortness of the glabella, the anterior margin of which barely projects in front of the fixed cheek. The Östersjö Limestone specimen is an original of Wiman (1908, p. 135, pl. 8, figs. 28-32). I have examined the other cranidium (IPU Nr. B161/Ar1311) figured by that author (1908, pl. 8, fig. 29) as Calymene trinucleina and it also shows the same distinguishing character. In addition, the anterior margin of the fixed cheek is directed inward and slightly backward, whereas in other upper Ordovician species it runs inward and slightly (or strongly) forward.

On the basis of these characters the N Baltic and Kullsberg specimens have been grouped together informally. Their other features are similar, but two specimens (from different localities and horizons - the Baltic specimen is somewhat older) is hardly an adequate sample for comparison. The comparatively short glabella of the Kullsberg cranidium may simply be due to the small size of this specimen. The Kullsberg individual has a more rounded 1p lobe than the Baltic specimen, and also appears to have a relatively more convex thoracic axis (tr.) and more rounded (sag. & exs.) thoracic axial rings and pleurae. A meaningful assessment of these differences is dependent on the availability of further material. The relatively larger palpebral lobe of the Kullsberg cranidium does, however, probably reflect the more immature nature of this specimen.

The material from the Dalmanitina Beds of Borenshult described as D. aff. D. drummuckensis can be distinguished from the present Kullsberg specimen through its relatively longer glabella, very broad lateral border furrow on the free cheek and shallower preglabellar furrow.

An interesting feature of the N Baltic specimen is the distribution of the fine tubercles and granules which form the surface ornamentation. These are abundant, uniform in size, and very closely spaced on the cranidium (excluding furrows), pygidial and thoracic axis, and outer part of the pygidial pleural region. In marked contrast on the thoracic pleurae and inner part of the pygidium these fine tubercles are considerably less abundant. Fine, close-set tubercles are present on the Kullsberg cephalon but the surface of the thorax is not well enough preserved to show the pattern of ornamentation.

Diacalymene diademata (Beyrich, 1846)

Plate 10, figs. 1-9; Plate 11, figs. 1-10.

1846 Calymene diademata; Beyrich, p. 24, pl. 2, figs. 4a, b, c.

1846 Calymene diademata BARR.; Barrande, p. 51.

1847 C. diademata; Hawle & Corda, p. 86.

1851 C. diademata; McCoy in Sedgwick & McCoy, p. 166.

1852 Calym. diademata. Barr.; Barrande, p. 567, pl. 19, figs. 11-19.

1927 Calymene (Diacalymene) diademata; Kegel, p. 617, text-fig. 2d, e.

1936 Diacalymene diademata (Barrande); Shirley, p. 396.

1949 D. diademata (Barrande); Bancroft, p. 309.

non 1957 Diacalymene diademata (Barrande), 1846; Tomczykowa, p. 137, pl. 3, fig. 5, pl. 4, figs. 1-3.

1959 Diacalymene diademata (Barrande); Whittington in Moore, p. 0452, fig. 353, 2a, b.

1962 Diacalymene diademata (Barrande); Dean, p. 113.

1970 Diacalymene diademata (Barrande); Tomczykowa, p. 72, ? fig. 5c.

1970 Diacalymene diademata (Barrande); Marek in Horny & Bastl, pp. 120, 121, pl. 16, fig. 6.

1971 Diacalymene diademata (Barrande, 1846); Whittington, p. 130, fig. 1c, d.

LECTOTYPE. Selected herein; incomplete cranidium; MB 498.1. B.K. p. 79. K.187; figured Beyrich 1846, pl. 2, figs. 4a, c, also herein Pl. 11, figs. 2, 6, 10.

TYPE STRATUM AND TYPE LOCALITY. From the Liten Formation, Wenlock Series, Svaty Jan, Czechoslovakia.

PARALECTOTYPES. Internal mould of pygidium, MB 499. 1. B.K. p. 79. K.183, figured Beyrich 1846, pl. 2, fig. 4b; internal mould of incomplete cranidium, MB 498.2. B.K. p. 79; internal mould of free cheek, MB 243. B.K. p. 74.

ADDITIONAL MATERIAL. Abundant material of this species is housed in the Narodni Museum, Prague. I have seen smaller, but representative collections of the taxon in the following British Museums: Royal Scottish Museum, Edinburgh, Sedgwick Museum, Cambridge, and National Museum of Wales, Cardiff.

DIAGNOSIS. Glabella weakly to strongly bell-shaped in outline. Lateral lobes 1p and 2p subquadrate. Preglabellar furrow very deep. Inward facing side of anterior border is very steeply inclined. Junction of border and furrow is strongly ridged. Sharp ridge also separates very steeply sloping outer side and inner sides of anterior border. In frontal view anterior border is quite strongly arched.

DESCRIPTION. Glabella about as long as wide, weakly to strongly bell-shaped in outline. Occipital ring narrows and bends forward behind lateral lobe 1p. Occipital furrow widest (sag.) medially. Large, subquadrate lobe 1p is one third as wide as glabella, has well rounded abaxial margin and angular anterior abaxial corner. Furrow 1p extremely narrow and deep between first two lateral lobes (in some specimens the sides of lobes 1p and 2p are in contact), runs inward and backward turning more sharply backward at inner corner of lobe 1p; shallow prolongation directed exsagittally to occipital furrow. Very much shorter, shallower anterior branch of furrow 1p runs up inner side of lobe 2p. On adaxial side of posterior branch central glabellar area is very faintly inflated. Lobe 2p subrectangular, long axis trending forward and outward, outer margin very blunt - abutts against weakly projecting (tr.) genal buttress. Furrow 2p as narrow as furrow 1p, deep, trends inward and slightly backward. Transversely elongate lobe 3p is quite strongly swollen, clearly defined anteriorly by sharp furrow 3p. Weak inflation in front of furrow 3p, but apparently no discrete 4p lobe. Subrectangular frontal glabellar lobe about $3\frac{1}{2}$ to 4 times as wide as long, anterior margin weakly arched in outline, reaches in front of fixed cheek. In lateral profile central area of glabella projects just above lateral lobes and clearly above fixed cheek, is gently convex upwards and approximately horizontally inclined from occipital furrow to furrow 2p, falls gently from latter to anterior margin of frontal lobe, descends vertically thereafter to preglabellar furrow.

Axial furrow very shallow next to occipital ring - directed forward and outward, around lobe 1p very narrow and deep, widening fractionally at furrow 1p, passes under bridge of lobe 2p and genal buttress, a deep channel beside lobe 3p and frontal lobe.

Preglabellar furrow slightly wider (sag. & exs.) than axial furrow, very deep,trench-like, undercutr frontal glabellar lobe, anterior side curves steeply upward and inward to meet strongly ridged posterior margin of anterior border. Latter proceeds upward and forward at unusually steep angle before turning sharply through less than 90 degrees to pass into broad, outer facing side which arches steeply downward and forward to rostral suture. In lateral profile outline of anterior border is chisel-edged; in frontal view highest part of anterior border is at median line, reaches above frontal lobe, slopes downward (often quite strongly) either side to facial suture. Anterior margin evenly convex forward.

Palpebral lobe centred opposite middle or anterior part of lateral lobe 2p. Inner, anterior corner of fixed cheek is drawn forward and inward to overhang very narrow furrow which separates cheek from swollen, distal part of anterior border; cheek and border almost touch at this point. Posterior branch of facial suture directed transversely outward, then swings backward to cross lateral border furrow after which it runs exsagittally for a very short distance before finally bending outward again to genal angle; anterior branch runs more or less straight forward to anterior margin then cuts inward and downward to broadly arched rostral suture. In frontal view outer facing slope of anterior border is wider sagittally than near facial suture.

Shallow depression separates eye socle on free cheek from convex inner region. Lateral border furrow not deep, better marked anteriorly than posteriorly. Lateral margin gently arched between facial sutures except where it curves more sharply backwards near genal angle.

Rostral plate unknown. Hypostome wider than long. Anterior margin arched forward; anterior border flexed ventrally; anterior pit deep. Between anterior and posterior wings lateral border is narrow and convex (tr.), posteriorly it expands into short, flat spine. Anterior lobe of median body rises from anterior border furrow, median furrow and lateral border furrows into a small, pointed, circular inflation. Median furrow very weak, particularly sagittally. Maculae not inflated, marked only by smooth oval area on the line of the median furrow. Posterior lobe crescent shaped, slightly less inflated than anterior lobe, falls most steeply to short (tr.) posterior border furrow.

Axis of pygidium contains five rings which are widest medially; fifth axial ring incompletely defined posteriorly. First four ring furrows complete, shallowest in central part of axis, become deeper and slit-like distally; fifth ring furrow incomplete. In internal moulds fifth ring furrow may be absent and all ring furrows are much wider (sag. & exs.) and shallower. Axis rises above pleural region and narrows gradually posteriorly to bluntly rounded terminal axial piece. There are five pleural furrows, each is well marked along its whole length and traverses between a half and two thirds the pleural region. Interpleural furrows much more weakly defined and fractionally longer than pleurals. Smooth border present inside lateral margin, but it is not bounded adaxially by border furrow. Lateral and posterior faces of postaxial sector inclined vertically to margin of pygidium.

More often than not cuticle is missing; where preserved surface ornamentation consists of rather fine, closely spaced tubercles.

DISCUSSION. It has been generally accepted that the author of Calymene diademata is Barrande (1846), but in the same year Beyrich also fully described and illustrated this species and, as Whittard (1960, pp. 136, 137) has pointed out in dealing with Pharostoma pulchrum, Beyrich has priority of publication. Therefore the species belongs to Beyrich and not Barrande. The binomen used by both Beyrich and Barrande was the same and the specimens used by each author are from the same locality and horizon. Barrande's material is housed in the Narodni Museum, Prague,and Beyrich's syntypes, from which a lectotype has here been chosen, in the Museum of the Humboldt University, E Berlin, D D R. Under article 74 (a)(i) of the I C Z N the lectotype designated by Marek (in Horny and Bastl 1970, p. 121) based on Barrande's material (NMP It335, CE 1251; figured Barrande 1852, pl. 19, figs. 12-14) is invalid.

Although several authors have made reference to D. diademata, this study represents the first modern revision of the species. Diagnostic is the very steeply sloping inner face of the anterior border, the very distinct 'ridge' at the break in slope separating anterior border from preglabellar furrow, the rather sharp angle (as seen in lateral profile) between the inner and outer sides of the anterior border, and the somewhat medially pointed outline (as seen in frontal view) of the most dorsal margin of the anterior border. In the latter feature it resembles Flexicalymene declinata (Hawle & Corda, 1847) from the Ashgill of Bohemia. Also characteristic is the absolute size of the species - this taxon has provided the largest cranidia in the genus.

D. diademata is readily distinguished from all other species, though its affinities lie more with the D. drummuckensis - D. consimilis stock rather than with the D. crassa group of species. It represents the only member of the genus yet described from the Silurian of Bohemia but Snajdr (1971, p. 16) has also recorded a Diacalymene species from the volcanic - carbonate facies of the Llandovery. The description of this species is awaited with interest especially with regard to any light it might throw on the derivation of D. diademata. Specimens of D. drummuckensis (Reed, 1906) sometimes have quite a steeply sloping inner side to the anterior border but it is never as strongly inclined as in D. diademata. Other differences of drummuckensis include its lower, less strongly arched anterior border (compare Pl. 4, fig. 3, with Pl. 11, fig. 4) the inner and outer sides of which meet each other at a greater angle (compare Pl. 4, fig. 2, with Pl. 11, fig. 2).

OCCURRENCE. D. diademata appears restricted to the upper Liten Formation of Bohemia. It has been recorded (Tomczykowa 1957, pl. 137, pl. 3, fig. 5, pl. 4, figs. 1-3) from the Wenlockian (Monograptus riccartonensis to Monograptus flexilis zones) of the Holy Cross Mountains but I cannot support the assignment of these specimens to the Bohemian species. It is most abundant at the type locality where it is associated with Cheirurus insignis Beyrich, 1845 and Staurocephalus murchisoni Barrande, 1846. Barrande (1852, p. 568) also lists the following Bohemian localities where it occurs: Listice near Beroun, Luzce, Lodenice and Ohrada.

Diacalymene allportiana (Salter, 1865)

Plate 9, figs. 4-6

1865 Calymene Blumenbachii, var. Allportiana; Salter, p. 97, text-fig. 20.

1888 Calymene Blumenbachii var. Allportiana Salt.; Etheridge (pars), p. 45.

1933 Calymene allportiana Salter, 1865; Shirley, p. 56, pl. 1, figs. 12-14.

1936 Calymene allportiana; Shirley, p. 400.

1970 C. allportiana SALTER, 1864; Schrank, p. 115.

HOLOTYPE. A complete individual; BM 58984; figured Salter 1865, p. 95; Shirley 1933, pl. 1; here Pl. 9, figs. 4-6.

TYPE STRATUM AND TYPE LOCALITY. Wenlock Limestone, Dudley, Worcestershire.

ADDITIONAL MATERIAL. None known.

DIAGNOSIS. Glabella bell-shaped, has small intermediate lobe. Axial furrow very wide around lobe 1p. Dorsal surface of anterior border separated from preglabellar furrow by very weak break in slope. In frontal view anterior border is very strongly arched. Anterior margin of cranidium projects somewhat forwards medially. Tubercles on inner, anterior part of fixed cheek and near genal buttress are much coarser than those on glabella.

DESCRIPTION. Cephalon is about twice as wide as long. Glabella is bell-shaped, longer than wide and just less than one third the cephalic width. Occipital ring is mostly destroyed except for distinct node at axial furrow. Lateral glabellar lobe 1p is relatively small, less than one third as wide as glabella, subcircular in outline and independently convex of central glabellar area.

From axial furrow the 1p furrow runs inwards and narrows (exs.) before bifurcating; posterior branch is directed more backwards before finally turning to be almost transversely oriented; anterior branch passes forwards and inwards over neck of lobe 2p. A small, rounded intermediate lobe lies within the fork of furrow 1p. Subcircular lobe 2p joined to genal buttress. Furrow 2p is directed inward and slightly backward to connect with anterior extension of furrow 1p. Lobe 3p is transversely elongate. Furrow 3p is distinct. Anterior margin of transversely subrectangular frontal glabellar lobe only weakly convex forwards, falls vertically to preglabellar furrow and projects beyond fixed cheek. Central area of glabella narrows gradually towards occipital furrow. In lateral profile glabella stands fairly well above fixed cheek.

Axial furrow very wide (tr.) around lateral lobe 1p, much less so next to lobes 2p and 3p, in front of the latter it is almost as wide as beside lobe 1p and it fans out on reaching preglabellar furrow. Moderately deep preglabellar furrow passes forwards and upwards with slight break of slope into anterior border. In lateral profile dorsal surface of anterior border is very weakly convex, it slopes forward and steeply upward before curving broadly over into its outer face which is inclined downward and backward; the highest point of anterior border stands above frontal glabellar lobe but not above central area of glabella, in dorsal view it projects beyond general cephalic outline and opposite each axial furrow it is distinctly swollen. In frontal view anterior margin is strongly arched.

Posterior side of posterior border furrow is very short (exs.) and steeply sloping; anterior side substantially less steep and much wider. Behind palpebral lobe fixed cheek is almost flat, moderately inclined (exs.); in front of palpebral lobe it is convex, anterior face descending vertically to abaxial extension of preglabellar furrow and inner corner slightly overhanging this furrow. Between palpebral lobe and genal buttress the cheek is gently inclined. Palpebral lobe centred opposite anterior margin of lobe 2p and seems about equal in length to lobe 1p; distance (tr.) between palpebral lobes about twice that across glabella at lobes 2p. Anterior branch of facial suture runs forward and marginally inward. Posterior branch directed transversely from eye lobe before curving posteriorly to cross lateral border furrow, and finally running more backward across lateral border to genal angle.

Narrow eye socle slopes vertically to convex, very steeply sloping main part of free cheek. Lateral border furrow is broadly U-shaped, fades approaching posterior branch of facial suture. Lateral border curves over and under to meet doublure. Hypostome unknown. Border sector of rostral plate badly disfigured.

Thorax has thirteen segemnts. Axis is wider than distance on each pleuron from axial furrow to fulcrum. Each axial ring is of near constant width (sag. exs.) and mildly convex in profile, at axial furrow swollen into prominent node. Articulating furrow U-shaped; articulating half-ring gently convex (sag.). Deeply incised, U-shaped pleural furrow separates higher and wider posterior from anterior pleural band. Posterior band forms bounding rim to articulating facet; this rim is better developed on posterior than anterior pleurae. Abaxially from fulcrum each pleuron is bent strongly downwards and faceted; the more anteriorly positioned pleurae have a well rounded posterior margin, on posterior pleurae this margin becomes more angular.

Pygidium has been abraded, especially on right pleural region, but at l tsix axial rings and five pleural furrows can be made out. Most anterior axial ring weakly inflated distally. Ring furrows are deepest a little inwards from axial furrow. Axis is moderat-ly convex (tr.). Axial furrow fairly shallow, becomes weaker posteriorly and is barely visible around bluntly rounded terminal axial piece. From axial furrow pleural region slopes at first quite steeply, then vertically to lateral margin. Fifth pleural furrow seems expanded in its outer part to form sides of postaxial sector. Pleural region has at least four pleural furrows. Weakly impressed pygidial cincture runs onto posterior margins of thoracic pleurae.

Ornament of glabella, outer part of fixed cheek and free cheek (except furrows) consists of rather closely spaced small to medium-sized rounded tubercles and granules. In addition to these projections, inner part of fixed cheek anterior to lobe 1p has coarser, more irregularly shaped tubercles. A few tubercles are scattered over rest of exoskeleton, the surface of which has been considerably 'polished'. Articulating facets of pleurae covered with numerous, tightly-set granules.

DISCUSSION. considering the abundant calymenid material from Dudley, it is surprising that the holotype of this species is the only known specimen. Shirley (1933, p. 58-59) placed allportiana in Calymene and noted its resemblance to C. nodulosa Shirley, 1936. The latter taxon has been made (herein Chapter F) the type species of a new genus which is partially diagnosed by having a glabella shorter than its fixed cheeks.

Though weakly defined, there is a faint break in slope between the anterior border and preglabellar furrow in allportiana, and I prefer to regard it as belonging to Diacalymene rather than to Calymene. Other features which contribute towards this assignment include the fine, closely-set glabellar tubercles, the swollen nature of the anterior border opposite the axial furrow, and the slight inwards projection of the fixed cheek.

D. diademata is like D. allportiana in its quite strongly arched anterior border (cf. Pl. 9, fig. 4, Pl. 11, figs. 4, 6). The group of characters by which allportiana is distinguished from diademata and other congeneric species are given above (diagnosis).

OCCURRENCE. Only the type locality.

Diacalymene crassa Shirley, 1936

Plate. 12, figs. 1-10; Plate 13, figs. 2, 4, 5, 9, 13.

1936 Diacalymene crassa sp. nov.; Shirley, p. 416, pl. 29, figs. 21-23.

1949 D. crassa Shirley; Bancroft, p. 309.

1961 D. crassa; Wolfart, p. 71.

? 1970 Diacalymene sp. (? crassa Shirley, 1936); Temple, p. 64, pl. 18, figs. 13-20.

HOLOTYPE. Incomplete internal mould cranidium; GSM 54910 (formerly GSM Pg2364); figured Shirley 1936, pl. 29, figs. 21, 22, and here Pl. 12, figs. 1-3, 5.

TYPE STRATUM AND TYPE LOCALITY. Gasworks Mudstone, upper Rhuddanian Stage, Llandovery Series, by the side of Frolic path, 383-390 yards from Higgons Well, half a mile SE of Haverfordwest, S Wales.

ADDITIONAL MATERIAL. About a dozen specimens, most of which are internal mould cranidia, and also including one cephalon and one complete specimen. This material is in the Sedgwick Museum, Brit. Mus. Nat. Hist. and Geol. Surv. Mus.

DIAGNOSIS. Glabella weakly bell-shaped to sub triangular in outline, quite strongly convex (tr.). Frontal glabellar lobe subsemicircular in outline, projects well in front of fixed cheek. Preglabellar furrow only moderately deep. Anterior border rather long. Anterior margin quite strongly arched forwards (dorsal view).

DESCRIPTION. Cephalon slightly more than twice as wide as long. Glabella noticeably convex (tr.), outline weakly bell-shaped to subtriangular. Occipital furrow on internal mould is fairly deep and rather broad(sag.). Lobe 1p projects distally beyond lobe 2p, is quite strongly inflated, subovoid to subcircular in outline, is less than one third as wide as glabella. Furrow 1p deep at axial furrow, runs inwards and swings progressively more backwards around lobe 1p. No discrete intermediate lobe. Subcircular lateral lobe 2p semi-isolated from central glabellar area by shallow furrow, joined to genal buttress. Lateral furrow 2p present only on side of glabella. Small, elongate (tr.) lobe 3p merges dorsally with central glabellar area; furrow 3p faint. Some specimens (holotype and GSM 54911) show evidence of weakly convex 4p lobe. Frontal glabellar lobe subsemicircular in outline, dorsal surface stands well above anterior border, is undercut by preglabellar furrow, projects considerably beyond fixed cheek. In lateral profile glabella is distinctly elevated above fixed cheek, between lobes 1p and 2p it is gently convex and horizontally inclined or sloping very gently forwards and downwards; in front of lobe 2p it falls towards preglabellar furrow at first in a broad arc, becoming gradually steeper and finally slopes downwards and backwards as anterior face of frontal lobe.

Axial furrow shallowest beside occipital ring, becomes much deeper anteriorly towards lobe 2p as fixed cheek rises upwards quite steeply from posterior border furrow to genal buttress; furrow is still relatively deep at lobe 3p opposite which its outer, almost vertically sloping wall is abaxially convex in dorsal view. Anterior pit situated in base of axial furrow below frontal lobe. Preglabellar furrow only moderately deep, anterior side meeting long anterior border which then projects very gently forwards and upwards. Division between preglabellar furrow and anterior border marked by a strong break in slope which is less well developed on internal moulds and best defined on all specimens opposite (exs.) side of frontal glabellar lobe. Anterior border of uniform width (sag. & exs.) except opposite axial furrow where it is slightly wider and very mildly inflated. Anterior margin quite strongly convex forwards.

Fixed cheek in front of palpebral lobes steeply down (exs.) to shallow anterior continuation of lateral border furrow; the inner, most anterior corner of cheek is somewhat pointed and projects slightly forwards and inwards over this furrow towards anterior border. Palpebral lobe centred opposite middle of lateral lobe 2p; situated on highest part of fixed cheek and relatively close to axial furrow. Posterior branch of facial suture imperfectly known, runs outwards and a little backwards from eye lobe before turning towards genal angle Anterior branch, directed fractionally forward and inward to anterior margin before running across ventrally facing slope of anterior border to meet rostral suture. Rostral plate seen in one internal mould specimen (Pl. 12, fig. 6) rostral suture parallelsanterior margin of cranidium; connective sutures abaxially convex, posteriorly convergent inner arc of border sector more highly vaulted than rostral suture. Inner part of free cheek slopes very steeply to shallow lateral border furrow. Lateral border is convex, its upper part vertically sloping, its lower part curving over and under to meet upward and outward sloping doublure at acute angle.

Thorax and pygidium known only from internal moulds. Thorax has thirteen segments. Axis is very convex (tr.) stands well above slightly narrower (tr.) pleural region. Axial ring swings forwards near axial furrow, the more anterior ones appear slightly inflated distally. Pleuron of normal calymenid type, pleurae bend down at right angles abaxially from fulcrum.

Pygidium about twice as wide as long. Axis fairly convex (tr.), has at least five axial rings and rounded terminal axial piece. Ring furrows shallowest axially. Pleural region has five pleural furrows. Interpleural furrows best marked near lateral margin, fade rapidly towards axial furrow.

External ornamentation poorly preserved and ill-known; a few small scattered tubercles on glabella and anterior border.

DISCUSSION. Specimens here assigned to D. *crassa* show a reasonable amount of variation in certain cranidial characters but I have preferred to regard all as belonging to one species, especially as some of the observed differences (from the holotype) may be more apparent than real due to the effects of distortion. At the same time it may be noted the holotype is the only specimen I have available from the type locality; the other specimens are from the Gasworks Mudstone of nearby localities in the Haverfordwest district. A complete internal mould individual of crassa (Pl. 13, fig. 5) shows a more steeply inclined anterior border than that of the holotype and the 'ridged' break in slope from preglabellar furrow to anterior border is not marked. But the preglabellar area of this specimen has been subject to some discomposure, and the posterior margin of the doublure sector of the rostral plate (or anterior margin of the hypostome) has intruded on to the dorsal surface of the cranidium, thus obliterating the contact of preglabellar furrow and anterior border. Although the preglabellar furrow of this species is never deep, in one cranidium (Pl. 12, fig. 8) it is particularly shallow but other characters of this specimen are in agreement with those of the holotype and I have also referred it to D. crassa. None of the cranidia examined show a discrete intermediate lobe at the inner end of lateral furrow 1p though the glabellar side is sometimes faintly swollen (Pl. 1, fig. 1).

Several species have been questionably referred to or compared with D. crassa. In his paper on the stratigraphy and fauna of the Silurian and Devonian of Paraguay, Wolfart (1961, p. 71, pl. 4, fig. 1) figures an internal mould cranidium which he referred to as D. cf. crassa. Opinion has varied as to the age of the beds in which this specimen was found (Wolfart 1961, p. 30). Harrington (in Jenks 1956) favoured a lower Devonian age whereas on the basis of the faunal evidence Wolfart concluded they were lower Llandovery. The poor preservation of the South American cranidium prevents a detailed comparison with D. crassa but there is little doubt that in its well rounded frontal glabellar lobe and glabellar outline it closely resembles the Welsh species. Temple (1970, p. 64) has discussed material from the high Rhuddanian of Meifod, Montgomeryshire which he referred to as Diacalymene sp. (? crassa Shirley, 1936). On the basis of the cranidial characters the Meiford taxon undoubtedly belongs in the crassa group of species. The pygidium of D. crassa was undescribed at the time of Temple's study. The examples that author figures are much less abraded than the one illustrated here (Pl. 13, figs. 5, 9, 13) but they are similar in general form and number of axial rings and pleural furrows. Specimens of Diacalymene from the Llandovery (Stage 6b) of the Oslo-Asker district, Norway are compared with D. crassa below.

D. crassa is very closely related to D. gibberosa sp. nov. from the lower Llandovery of Norway and a discussion of the two taxa will be found under the latter species.

There is little to separate crassa from some of the specimens referrred herein to D. marginata, but as a whole the Llandovery population has a more subsemicircular outline to the frontal lobe and a more subtriangular glabellar outline. However a taxon from the Silurian of the United States, which must be referred to Diacalymene, bears such a strong resemblance to the Welsh species that they may even be conspecific. Foerste described and illustrated his species Calymene vogdesi several times (1885, pp. 109-12, pl. 8, fig. 25, ? fig. 24; 1887, pp. 95-98, pl. 8, figs. 12-16; 1893, p. 526, pl. 25, fig. 25, ? fig. 24, pl. 27, figs. 12-15), and the type specimen, from Centreville, Ohio, appears to be in rocks of Llandovery age. Clearly D. vogdesi (Foerste, 1887) is in need of further investigation.

Lastly, it is worthy of note that the monotypic genus Spathacalymene Tillman 1960, type species S. nasuta (Ulrich, 1879), from the upper Llandovery of Indiana has essentially the same type of preglabellar area as in Diacalymene, but just a longer anterior border.

It would not be unreasonable to suggest that the American genus was derived from a Diacalymene species of lower or middle Llandovery age.

OCCURRENCE. Gasworks Mudstone, Rhuddanian Stage, Llandovery Series, Haverfordwest area, S. Wales.

Diacalymene cf. D. crassa Shirley, 1936.

Plate 13, figs. 1, 3, 8.

MATERIAL. Eight internal moulds of incomplete cranidia, PMO 65535, PMO 88647, PMO 88872 (two specimens), PMO 88873, PMO 88877, PMO 88881, PMO 91112; one external mould of an incomplete cranidium, PMO 65532. All the material was collected by N. Spjeldnaes except PMO 91112 which was collected by J.F. Bockelie.

OCCURRENCE. PMO 91112 is from Stage 6 (Lower Llandovery), Vakas, ved Jernbanelinjen, Asker district of the Oslo Region, Norway. PMO 65532, PMO 65535, PMO 88647, PMO 88881 are from Stage 6b (lower Llandovery), Gullerasen, Oslo district, Norway. PMO 88872, PMO 88873, PMO 88877 are from Skaering between Grakammen and Gullerasen, Oslo district, Norway.

DISCUSSION. Several internal moulds from the lower Llandovery of the Oslo district are all considered to belong to one species within the crassa group. This species shows several characters which ally it closer to D. crassa than to D. gibberosa sp. nov. For example lateral glabellar lobe 2p is semi-isolated from the medium glabellar lobe by a shallow furrow, the inner, anterior corner of the fixed cheek is a little pointed - projecting somewhat towards the anterior border, the outline of the frontal lobe between 3p furrows is less arcuate than in gibberosa, and the ridged boundary between preglabellar furrow and anterior border is more distinct (compare Pl. 12, fig. 9; Pl. 13, figs.

1, 3, 6). The Norwegian specimens are incomplete and not (except for PMO 91112) well preserved but seem to differ from D. crassa in having a somewhat longer preglabellar furrow; they may eventually be recognised as a geographical subspecies of the Welsh taxon.

Diacalymene gibberosa sp. nov.

Plate 13, figs. 6, 7. 10-12; Plate 14, figs. 1-16.

DERIVATION OF THE NAME. From the Latin, gibberosus, humpbacked or swollen, referring to the nature of the glabella.

HOLOTYPE. Incomplete cranidium; PMO 41620; coll. J. Kiaer; Pl. 14, figs. 1, 2, 4.

TYPE STRATUM AND TYPE LOCALITY. Stage 6aβ(lower Llandovery), Silurian, uppermost layer of the eastern headland, south side of Sjursøya, northern end of Bunne fiord, Oslo district, Norway.

ADDITIONAL MATERIAL. Numerous cranidia, free cheeks, pygidia and thoracic segments, and one external cast of a hypostome, all of which are contained in blocks of a bioclastic limestone. PMO 20945-48, PMO 41619, PMO 41621-627, PMO 41632-37, PMO I0838, PMO 91111, PMO 91113, Coll J. Kiaer, 1905.

DIAGNOSIS. Glabellar outline parabolic; lobe 2p not isolated from median glabellar lobe by a furrow; frontal glabellar lobe very short, arcuate in outline. Inner, anterior corner of cheek a little swollen, but not pointed.

DESCRIPTION. Cranidium about two and one third times as wide as long. Glabella less than one third as wide as cranidium, parabolic in outline, lobe 1p projects but a short distance beyond that of lobe 2p. Occipital ring gently to strongly convex in lateral profile, narrows gradually abaxially. Occipital furrow well incised and V-shaped behind central glabellar lobe, deeper and narrower (exs.) behind lateral lobe 1p. The latter is relatively small - only about a quarter as wide as glabella, and quite strongly swollen. Lateral furrow 1p very deep abaxially, in many specimens is directed inward a little before turning obliquely backward on inside of lobe 1p, in other specimens Pl. 14, fig. 1, it is straight and runs directly inward and backward from axial furrow; a shorter, exceedingly faint, anterior branch sometimes present (Pl. 14, fig. 9), runs forward, inward and upward on lower side of lobe 2p, fades out rapidly towards dorsal surface of glabella. No intermediate lobe. Lobe 2p relatively large, can be almost equal in size to lobe 1p, is not separated from central area of glabella by a furrow but appears as an inflated, broadly-based (exs.) abaxial extension of this area. Furrow 2p barely seen in dorsal view. Lobe 3p situated low down on glabellar side, protrudes little beyond ouline of frontal glabellar lobe. Distinct furrow 3p not visible in dorsal view. Very short (sag.), steeply sloping, bulbous frontal glabellar lobe juts in front of fixed cheek, is exceedingly well rounded and arcuate in outline as its abaxial margins progress immediately inwards and forwards from furrow 3p. Glabella is highly convex (tr.); sagitally it proceeds forwards horizontally from occipital furrow to posterior part of lobe 2p, in front of which it begins a highly curved descent through slightly more than ninety degrees to preglabellar furrow. Glabella stands prominently above fixed cheek. Axial furrow very shallow beside occipital ring, around 1p lobe it is deep, becoming more so towards furrow 1p, constricted in depth where lobe 2p meets buttress from fixed cheek, next to 2p furrow and 3p lobe it is slightly wider (tr.) than at lobe 1p with a similar steeply sloping outer wall, passes finally into preglabellar furrow. Anterior pit positioned at the bottom, inner side of axial furrow below lateral furrow 3p.

Fairley shallow preglabellar furrow fractionally undercuts frontal glabellar lobe, anterior side is moderately inclined forwards and upwards medially, becomes more steeply inclined abaxially. Anterior border wider (sag. & exs.) than preglabellar furrow, division between these two marked by break in slope, the flat to gently convex upper surface of the border extending forwards horizontally (Pl. 14, fig. 16) or slightly downwards (Pl. 14, fig. 1) before swinging over to the convex outer side of the border which runs down to rostral suture. Dorsal surface of anterior border does not reach the level of the lowest part of frontal glabellar lobe; opposite axial furrow than at median line. Anterior margin broadly arcuate between branches of facial suture.

Posterior border widens (exs.) considerably abaxially from fulcrum, between fulcrum and axial furrow is about half the width of occipital ring. Posterior border furrow deep, broadly U-shaped (exs.) with concave or flat-bottomed base, lens-like in outline between axial furrow and facial suture. Fixed cheek relatively flat and moderately inclined downwards from palpebral lobe to posterior border furrow; in front of eye lobe fixed cheek is gently convex, falls steeply to shallow anterior extension of lateral border furrow, inner anterior corner of cheek weakly swollen but does not project over this furrow towards anterior border. In frontal view uppermost surface of fixed cheek is gently convex, about horizontal from palpebral lobe to short (tr.) genal buttress. Palpebral lobe centred opposite middle of lobe 2p and about as long (exs.) as adaxial part of that lobe, slopes very gently downward to fixed cheek. Posterior branch of facial suture directed outwards from palpebral lobe before turning sharply backwards to cross posterior part of lateral border furrow, finally it turns again more posteriorly and runs to genal angle. Anterior branch of suture is straight, directed forward and slightly inward to anterior margin, on outer side of anterior border it runs inward and downward to rostral suture.

Free cheek bears eye socle below visual surface of eye; main part of cheek is moderately convex (tr.) and rather narrow; lateral border furrow broadly U-shaped; broad lateral border is more steeply sloping near anterior than posterior branch of facial suture, curves over and under to meet doublure.

Rostral plate unknown. Hypostome known from one small external mould (Pl. 14, fig. 6). Anterior border reflexed ventrally; anterior border furrow very broad (sag.). Anterior pit well marked. Lateral border convex (tr.), narrows slightly posteriorly, broadens behind latter into posterior spine. Anterior lobe of median body slightly inflated in its central portion, about twice as long as posterior lobe. U-shaped median furrow best marked near anterior part of lateral border, weakest posteriorly. Maculae apparently lacking. Posterior lobe crescent shaped.

Axial ring (pl. 14, figs. 3, 7) of thoracic segment quite strongly convex (sag. & exs.), maintains constant width from median line to axial furrow where it is somewhat flexed forward. Articulating half-ring two thirds the width (sag.) of axial ring. Posterior pleural band well rounded in section, at least twice as wide (exs.) as anterior pleural band. Pleural furrow U-shaped, narrows distally and runs forwards onto flat articulating facet before dying out. Narrow articulatory shelf runs along anterior edge of pleuron from axial furrow to panderian notch.

Axis of pygidium almost flat in section (tr.), has five, rarely six axial rings. First four ring furrows substantially deeper at axial furrow thanmedially, fifth ring furrow sometimes lacking medially (especially on large specimens), some specimens show faint trace of sixth ring furrow confined to central part of axis. Axial furrow relatively shallow, especially around terminal axial piece which falls smoothly and vertically to postaxial sector. Inner part of pleural region moderately inclined downward and outward, outer part much steeper - almost vertical to lateral margin. First four pleural furrows best marked at mid-length, do not quite reach lateral margin; fifth pleural furrow defined only along anterior edge, posteriorly it merges into a broad depression which form vertical, outward facing side of postaxial sector. Interpleural furrows weak at axial furrow, very weak at mid-length, deepest and clearly marked distally.

Surface of glabella covered with small tubercles of about constant size; these tubercles also present on anterior border and fixed cheek but here they are more scattered. All furrows on cranidium lack tubercles. Tubercles on free cheek similar to glabella. Top of axial ring bears small tubercles, articulating facet pustules, abaxial part of axial ring, posterior and anterior pleural bands appear smooth. On pygidium inner part of pleural region and abaxial part of axial rings seem more or less smooth, rest of pleural region finely tuberculate.

DISCUSSION. D. gibberosa has only been found in the lower Llandovery strata of the Sjursøya peninsula, near Oslo, Norway. The excellently preserved material forms part of the Silurian collections of J. Kiaer. All localities on Sjursøya have since disappeared under and industrial complex and it is fortunate that an adequate number of specimens are available to enable description of this most unusual species.

There is a considerable difference in appearance in the preglabellar area between internal and external mould specimens of this species. The internal mould shows little of the distinct anterior border and almost nothing of the break in slope which forms the boundary between anterior border and preglabellar furrow. Nevertheless the species is so distinct it can be readily recognised from both internal and external mould forms (compare Pl. 12, fig. 8 with Pl. 13, fig. 6).

The trend towards having a rather convex glabella (as exhibited by D. crassa) is carried to an extreme in D. gibberosa where the glabella is highly vaulted - both sagittally and transversely. Several other characters serve to distinguish gibberosa from crassa: it has a parabolic glabellar outline, the 1p and 2p lateral glabellar lobes are more equal in size the unusual shape of lobe 2p which is not isolated from the central glabellar area by a furrow, the frontal glabellar lobe appears sagittally shorter and consequently its outline is more arcuate (rather than semicircular) with virtually no abaxially facing sides, a generally more weakly arched (dorsal view) anterior margin, less strong break in slope between anterior border and preglabellar furrow, and it has a gently swollen (but not pointed) inner, anterior corner to the fixed cheek.

A further point of interest concerning D. gibberosa is the remarkable contrast between the convexity of the cranidial characters compared with those of the pygidium. For example the difference between the inflation of the glabella and the pygidial axis.

D. crassa, D. gibberosa and associated taxa form a good species group and appear to be stratigraphically useful as indicators of strata of Llandovery age.

OCCURRENCE. All the material was obtained from the eastern headland, south side of Sjursøya, northern end of Bunne fiord, Oslo district, Norway. Most of the specimens are specifically labelled as coming from Stage 6aβ. Others are more simply given as occurring in Stage 6 but it is fairly safe to assume (largely on lithological grounds - they all occur in a very distinctive, trilobite - rich bioclastic limestone) that all were collected from the same horizon (6aβ). Bassett and Rickards (1971, p. 254, fig. 1) have correlated the Llandovery and Wenlock successions of the nearby island of Malmøya with the British graptolite divisions but they only dealt with beds as low as 6bβ - which was considered coeval with the lower part of the _convolutus_ Zone (= Idwian). In assessing the age of 6aβ on Sjursøya one must bear in mind that these authors have demonstrated some of Kiaer's (1908) Stages within the Oslo district to be diachronous, but Stage 6aβ on Malmøya would appear to be no younger than the _gregarius_ Zone (=lowermost Idwian).

THE GENUS CALYMENE FROM THE SILURIAN AND LOWER DEVONIAN OF BRITAIN, SWEDEN AND CZECHOSLOVAKIA.

The type and other specimens of all hitherto erected species of Calymene from Britain, Sweden and Czechoslovakia have been examined. Most of the material studied from Sweden is housed in the Riksmuseum, Stockholm, and that from Bohemia in the Narodni Museum, Prague; much of the material from Britain is housed in the British Museum, though other museums (Sedgwick Museum, Hunterian Museum, National Museum of Wales etc.) and the Geological Survey have kindly entrusted me with substantial collections. Museum specimens have been supplemented, wherever possible, by my own field collections.

TERMINOLOGY, TECHNIQUES AND MEASUREMENTS.

These are the same as those outlined in the first part of this thesis.

SYSTEMATIC PALAEONTOLOGY.

Subfamily CALYMENINAE Milne-Edwards, 1840

Genus CALYMENE Brongniart, 1822

TYPE SPECIES. Calymene blumenbachii Brongniart, 1822, p. 11, pl. 1, figs. 1A-D; from the Wenlock Limestone of Dudley, England. By original designation of Brongniart 1822, p. 2.

OTHER SPECIES. C. antigonishensis McLearn, 1924; C. altirostris Foerste, 1923; C. aquatica sp. nov.; C. arotia Haas, 1968; C. aspera Shirley, 1936; C. boettneri Harrington, 1950; C. bowiei Gill, 1945; C. breviceps Raymond, 1916; C. camerata Conrad, 1842, C. carlops Lamont, 1949; C. cedarvillensis Foerste, 1919; C. clavicula Campbell, 1967; C. conspicua Schmidt, 1894; C. cresapensis Prouty, 1923; C. eximia sp. nov.; C. falcata sp. nov.; C. frontosa Lindström, 1885; C. interjecta Hawle & Corda, 1847; C. kashmirica Gupta, 1967; C. killarensis Gill, 1945;

	BRITAIN Stratigraphy	BRITAIN Calymene species	BOHEMIAN Stratigraphy	BOHEMIAN Calymene species	GOTLAND Stratigraphy	GOTLAND Calymene species
			Pragium	C. interjecta		
			Lochkovium			
	Downtonian		Přídolí-Schichten	C. interjecta		
Ludlow	Whitcliffian		Kopanina-Schichten / Budňanium		Sundre, Hamra	C. tentaculata campana
Ludlow	Leintwardinian	C. puellaris, C. lawsoni			Burgsvik, Eke	C. puellaris
Ludlow	Bringewoodian				Hemse	C. spectabilis, (?) C. eximia, C. patustria, C. neointermedia
Ludlow	Eltonian	Calymene sp2, C. aff. lawsoni, C. cf. neotuberculata		C. tenera		(?) C. spectabilis
Wenlock	upper	C. neointermedia, C. blumenbachii, C. aspera, C. cf. mimaspera, Calymene sp1, C. tuberculosa	Liten-Schichten		Klinteberg, Mulde, Halla	C. falcata, C. neotuberculata, C. tuberculosa
Wenlock	middle				Slite, Tofta	C. aquatica, C. aff. laevis, C. laevis
Wenlock	lower	C. aff. mimaspera			Högklint	
Llandovery	Telychian	C. carlops, C. hadyardensis			Upper Visby, Lower Visby	Calymene sp nov (?), C. frontosa
Llandovery	Fronian	C. subdiademata replicata			Not seen at surface	
Llandovery	Idwian	C. planicurvata, C. subdiademata subdiademata				
Llandovery	Rhuddanian					

Geographical and general stratigraphical distribution of *Calymene* species examined in the present study
Correlation of the British, Bohemian and Gotland Silurian after Cocks *et al.* 1971

Table 1

C. kokbaitalensis Maximova, 1968; C. laevigata Schmidt, 1907; C. laevis Lindström, 1885; C. lawsoni Shirley, 1962; C. macrocephala Prouty, 1923; C. mimaspera Schrank, 1970; C. minimarginata Schrank, 1970; C. neointermedia R. & E. Richter, 1954; C. niagarensis Hall, 1843; C. ohhesaarensis Schmidt, 1894; C. orthomarginata Schrank, 1970; C. patustria sp. nov.; C. planicurvata Shirley, 1936; C. platys Green, 1832; C. puellaris Reed, 1920; C. prenaica Balasova, 1954; C. restricta Prouty, 1923; C. scrivenori Kobayashi & Hamada, 1971; C. spectabilis Angelin, 1854; C. subdiademata McCoy, 1851; C. taimyrica Balasova, 1960; C. tenera Barrande,1852; C. tentaculata Schlotheim, 1820; C. tuberculosa Dalman, 1827; C. weberi Maximova, 1968.

Some of the species given in this list await revision; they may eventually fall into synonymy or be transferred to other genera.

DIAGNOSIS. Glabella more or less bell-shaped in outline, projects above & is level with (anteriorly) or protrudes in front of fixed cheek; it has three or four pairs of lateral lobes, only lobe 2p is papillate and joined to a genal buttress. Anterior border variably developed, runs smoothly posteriorly into preglabellar furrow. Hypostome has protruberance on anterior lobe of median body. Thorax has twelve (rare) or thirteen segments. Pygidium has between five and nine axial rings, five or six pleural furrows.

DISCUSSION. Calymene is compared with Diacalymene Kegel, 1927 and Tapinocalymene gen. nov. elsewhere (see previous and following chapters).

Whittington (1971) has recently revised Papillicalymene Shirley, 1936 from the Ludlovian of Gotland and discussed its relationship with Calymene; a few extra comments may be added here. In addition to P. papillata Lindström, 1885 and P. excavata Lindström, 1885, there exists a third (unnamed) species of Papillicalymene on Gotland which is morphologically less 'advanced' than either of the other two, in having no papillation at the anterolateral corner of the frontal glabellar lobe. In this respect it is the same as species of Calymene, and therefore one of the differences between Calymene and Papillicalymene no longer applies, and Whittington's (1971, p.462) diagnosis of the latter must be slightly emended accordingly. A strongly upcurved anterior border was also considered (Whittington 1971, p.463) a distinguishing character of Papillicalymene, but this type of border is also present in Calymene (see C. frontosa, C. carlops and Calymene sp. nov.? below). The most diagnostic characters of Papillicalymene seem to be the papillate 3p lobe and corresponding genal buttress, and the great disparity in width of the axial furrow beside lobe 1p compared with its width in front of this point. There is little doubt that Papillicalymene was derived from Calymene(Whittington 1971, p.464).

Of the more recent authors, Shirley (1933 and 1936), Campbell (1967), Whittington and Schrank (1970) have contributed most to our understanding of Calymene. Schrank has identified six species groups based on the nature of the anterior border. From the present study it is concluded that several of these groups (numbers 1, 4, 5, and 6) are fairly homogeneous units, and that the species included in each group can often be associated on other characters besides the anterior border. For example the form of the thoracic pleurae in C. spectabilis and C. laevis (group six) is quite different to that in C. blumenbachii and C. clavicula (group four). However certain species placed in group two do not appear to me to be closely related: Calymene nodulosa Shirley, 1933 is quite distinct in almost every character from, say, C. aspera and I have (elsewhere) made nodulosa the type species of Tapinocalymene gen. nov.. Similarly it is here considered unlikely that Calymene pompeckji Kummerow, 1928 belongs in the genus Calymene (see discussion of C. neointermedia).

Some of Schrank's groupings (for instance groups 1 and 4) have a stratigraphical as well as a morphological basis, and at least two of the groups (C. blumenbachii group (4) and C. tentaculata group (3))can be morphologically related to each other. Some of the species contained in the groups have herein been placed in synonymy (eg. C. lata Shirley, 1936), others (eg. C. ohhesaarensis Schmidt, 1894) are in need of revision. The detailed morphology of many of the taxa commented on by Schrank, is treated below in the species discussions.

OCCURRENCE. The stratigraphical range of Calymene is from the lower Llandovery to the lower Devonian. The genus has been recorded from Europe, N and S America, Asia, Australia and N Africa. Its presence in N Africa (Pillet 1968) is here regarded with doubt.

Calymene is well represented in Britain (especially in the upper Wenlockian) where it ranges from the upper Rhuddanian to the Whitcliffian.

In Bohemia it first makes its appearance in the lower Ludlovian (C. tenera) and extends into the Pridoli and lower Devonian with C. interjecta.

On Gotland Calymene ranges from the Lower Visby Beds (topmost Llandovery) to the Sundre Beds- that is the whole of the supramarine Silurian succession.

Calymene subdiademata subdiademata McCoy, 1851

Plate 1, figs. 1-14; Plate 2, figs. 7, 9.

1851 Calymene subdiademata (McCoy); McCoy (pars), p. 166 non pl. 1F, figs. 9,10.

1851 Calymene Blumenbachii Brong.; Salter in Murchison, p. 171.

1873 Calymene Blumenbachii, Brongn.; Salter (pars), p. 77.

? 1879 Calymene Blumenbachii, Brongniart; Nicholson & Etheridge, p. 140, pl. 10, fig. 6, non figs.2-5.

1906 Calymene blumenbachi, Brongniart, 1822; Reed, p. 133, pl. 17, figs. 12, 13.

1933 Calymene subdiademata McCoy, 1852; Shirley, p. 65.

1936 Calymene replicata sp. nov.; Shirley (pars), p. 411, non pl. 30, figs.2-5.

LECTOTYPE. Here selected; internal mould of incomplete cranidium; SM A34872; described McCoy 1851, p. 166 (pars); figured here Pl. 1, fig. 9.

TYPE STRATUM AND TYPE LOCALITY. Here restricted. Small cutting E of Newlands Farm (NS 27750434), Newlands, one mile N of Wallacetown, Girvan district, Ayrshire. Newlands Formation (Idwian) Llandovery Series.

ADDITIONAL MATERIAL. There are numerous (more than 50) topotype specimens of this species in the major British Museums, in particular the British Museum (Gray Collection) and Hunterian Museum, Glasgow. No attempt is made to list all the material.

DIAGNOSIS. Glabella very weakly bell-shaped, about 1.1 - 1.3 times as long as wide. Preoccular part of fixed cheek narrow - only about one fifth to one quarter as wide as glabella at lobe 2p. Axial furrow narrow (tr.). Preglabellar furrow moderately wide and deep. Anterior border moderately to strongly upturned, dorsal surface convex (sag.). Hypostome with small subcircular projection. Tubercules on cranidium fine and closely spaced.

DESCRIPTION. Cephalon about 1.7 - 1.8 times as wide as long. Slender glabella is about 1.1 - 1.3 times as long as wide, very weakly bell-shaped in outline, projects strongly in front of and reaches well above fixed cheek. Occipital ring gently swollen into small node at axial furrow. Lateral lobe 1p slightly less than one third as wide as glabella, subrectangular in outline (more rounded in internal moulds), does not protrude very much abaxially beyond lobe 2p. Lateral furrow 1p curves inwards and backwards, extends over 'neck' of lobe 1p as shallow depression; very weak anterior branch crosses inner side of subcircular lobe 2p which is joined to genal buttress. No intermediate lobe at adaxial end of furrow 1p. Lobe 3p transversely elongate, stretches down side of glabella. Fourth lobe weakly indicated on many specimens. Frontal lobe is bluntly to quite strongly rounded in outline.

Axial furrow deep and extremely narrow around lobe 1p, slightly wider between furrow 2p and frontal lobe. Anterior pit sited on inner side of axial furrow below posterior margin of frontal lobe or 4p furrow. Preglabellar furrow moderately deep and wide (sag. & exs.), sharply undercuts frontal lobe of glabella; anterior side of furrow curves forwards and moderately to strongly upwards. Anterior border is slightly wider (exs.) opposite axial furrow than medially, in section its dorsal surface is convex, in most specimens it runs smoothly posteriorly into the preglabellar furrow though in a few cranidia there is a slight edge between the two; outer side of border curves downwards, or downwards and slightly backwards to rostral suture.

Posterior margin of fixed cheek swings strongly backwards abaxially from fulcrum. Posterior border furrow fairly wide (exs.), distinctly impressed. Outer part of fixed cheek swings quite strongly downwards and backwards so that in some specimens genal angle lies behind occipital ring. Palpebral lobe is about as long (exs.) as and centred opposite lobe 2p. Preoccular part of fixed cheek very narrow (tr.) - about one fifth to one quarter as wide as glabella at lobe 2p, descends quite steeply forwards, its inner anterior corner may be slightly pointed.

Posterior branch of facial suture runs transversely for a short distance before turning sharply backwards to lateral border where it swings firstly more backwards and finally faintly outwards to posterior margin; anterior branch trends forwards to anterior margin.

Hypostome (BM It9091) 1.1 times as wide as long (sag.). Anterior margin very narrow, reflexed ventrally. Anterior lobe about four times as long as posterior lobe, has subcircular projection situated one third of the distance from anterior margin to exceedingly faint median furrow. Maculae quite strongly swollen. Lateral border furrow fairly deep. Posterior border extended into two short spines; posterior margin U-shaped.

Thorax has thirteen segments. Each axial ring swollen into a small node at axial furrow.

Axis of pygidium quite strongly convex (tr.), has at least six axial rings the anterior two of which are very slightly swollen abaxially. Axial furrow well marked. Pleural region bends strongly downwards, has five distinctly impressed pleural furrows; interpleurals best marked distally, very weak or absent proximally.

Ornament on glabella, fixed cheek and anterior border consists of very fine, closely spaced tubercules.

DISCUSSION.

History of the species. Calymene subdiademata was revised by Shirley (1933) who examined two of McCoy's specimens (SM A6806-807) and on account of their inadequate preservation declared the species a nomen dubium. In the Sedgwick Museum there are eight calymenid specimens which, according to catalogue information, all formed the basis for McCoy's (1851, p. 166) description of subdiademata. McCoy did not indicate any of these specimens as "the type" and they must all be regarded as syntypes; each is from a locality recorded by McCoy (1851, p. 167) as yielding his new species.

The syntypes, catalogue information and present determinations are:

1. & 2. SM A38377 - 378; Upper Bala, Coed Sion, Llangadoc, S Wales. These two internal moulds are incomplete cranidia of an indeterminate species of Calymene.

3. SM A41862; Upper Bala Schists, Pwllheli. Internal mould of a small, incomplete cranidium of a Flexicalymene.

4. SM A43426; Coniston Limestone, High Haume, Dalton in Furness, Cumberland. Very badly distorted internal mould of a cranidium. Possibly belongs to Gravicalymene; species indeterminate.

5. SM A6806; Calcareous Schists, Coniston Water-Head. Squashed, almost complete individual, possibly formed the basis for McCoy's pl. 1F, figs. 10, 10a. Mentioned by Shirley (1933, p. 65) as "reminiscent of C. quadrata King", but on further preparation is best referred to D. cf. marginata Shirley, 1936.

6. SM A6807; Calcareous Schists, Coniston Water-Head. Flattened internal mould of an incomplete cranidium. Can be referred to Gravicalymene, probably close to jugifera Dean, 1962.

7. & 8. SM A34872 - 873; Upper Bala (Caradoc), Mulloch, Dalquharran. These two incomplete cranidia (internal moulds) are considered conspecific and can be referred to Calymene. One specimen (SM A34873) is preserved in a sandstone similar to those I have seen from the Mulloch Hill Formation (= upper Rhuddanian; Cocks & Toghill 1973, p. 238) of the Craighead Inlier, Girvan; the other specimen is preserved in a reddish coloured sandstone which is unmistakeably the same as those from the Newlands Formation (= lower Idwian) of the Girvan district. Out of all McCoy's syntypes the last specimen is the most suitable to serve as the lectotype of subdiademata because its provenance can be accurately delimited, and there are many other extant specimens of the same species which allow an adequate definition of the taxon. It is apt that Salter (in Murchison 1851) should record "Calymene Blumenbachii, Brong., from the Red Quarry (C. subdiademata of McCoy's list)" from the area N. of Dalquharran.

The specimen from Leintwardine which formed the basis for McCoy's pl. 1F, figs. 9, 9a, has not been traced.

Morphology and relationships of C. subdiademata subdiademata. The main characters of subdiademata subdiademata are given in the diagnosis. Variation in the anterior border of the Newlands Formation population is phylogenetically significant and the taxon probably represents the nearest member of the genus to Diacalymene. Of the many cranidia examined from this horizon most have an anterior border typical of Calymene, but some have a slight edge between the border and furrow, and in one specimen (BM In43652) the border is indistinguishable from that of Diacalymene species except it is somewhat more convex and shorter (sag.) than is normal. Other features shown by subdiademata subdiademata which are more characteristic of Diacalymene than Calymene include the very fine cranidial tubercules and the small, subcircular (not spine-like as in nearly all Calymene species) projection on the anterior lobe of the hypostome. The Newlands Formation population is interpreted as representing a link species between Diacalymene and Calymene (though as a whole being closer to the latter) and provides support for the idea of a gradual transformation, not saltation, from one genus to the other.

C. frontosa Lindström, 1885 (see below) from the Upper Llandovery of Gotland can be distinguished from C. subdiademata on numerous characters, including its much coarser cranidial ornament, deeper and narrower lateral and posterior border furrows, wider axial and preglabellar furrows, smaller more anteriorly sited palpebral lobes and conspicuously projecting corners to anterior part of the fixed cheek.

A comparison of C. subdiademata subdiademata with C. subdiademata replicata is given below.

OCCURRENCE. Mulloch Hill Formation (upper Rhuddanian) and Newlands Formation (Idwian) of the Girvan district.

Calymene subdiademata McCoy, 1851 replicata Shirley, 1936

Plate 2, figs. 1-6, 8, 10, 11.

1936 Calymene replicata sp. nov.; Shirley (pars), p. 411, pl. 30, figs. 2-5.

? 1938 Calymene replicata Shirley; Whittard, p. 88.

1970 Calymene replicata Shirley; Schrank, pp. 115, 119.

HOLOTYPE. Internal mould of incomplete cephalon and three attached thoracic segments, plus counterpart; SM A14922a-b; figured Shirley 1936, pl. 30, figs. 2, 3, 5, and here Pl. 2 , figs. 1-3, 6.

The counterpart (SM A14922b) and its gelatine impression are now reported missing.

TYPE STRATUM AND TYPE LOCALITY. Upper Llandovery (near the base of), at the sharp bend in the stream, 360 yards above the footbridge S of Lletty'-r-hyddod, near Llandovery, Carmarthenshire.

ADDITIONAL MATERIAL. About fifteen cranidia and pygidia, and two almost complete specimens. Some of the specimens have a few thoracic segments attached. Loaned by Dr. P. Lane, Univ. of Keele.

DISCUSSION. The external mould of the holotype of this taxon is now missing, and the few topotype external moulds I have at hand are distorted. Shirley (1936, p. 411) regarded the Newlands Formation Calymene (now = C. subdiademata subdiademata McCoy, 1851; see above) as conspecific with his new species from the Llandovery area, C. replicata. The above topotype specimens of replicata appear to be inseparable from many of the Newlands cranidia of subdiademata, though the dorsal surface of anterior border in the Newlands population, taken as a whole, is more broadly convex and stoutly developed. As the range of variation in the Welsh and Scottish samples seems to overlap, it is argueable whether this difference justifies formal separation of the two populations, but I have here treated replicata as a subspecies of subdiademata.

OCCURRENCE. Type locality and Idwian of the Bog Mine area, Shropshire.

Calymene frontosa Lindström, 1885

Plate 3, figs. 1-9; Plate 4, figs. 1-9.

1885 Calymmene frontosa n.; Lindström, p. 69, pl. 15, figs. 1-4.

? 1894 Caly. frontosa Lindström; Schmidt, p. 18, pl. 2, figs. 4, 4a, non figs. 5, 5a, 6, 7.

1936 Calymene frontosa Lindström; Shirley, p. 387.

? 1949 Calymene carlops sp. nov.; Lamont, p. 319, pl. 18, figs. 13-19.

? 1970 Calymene carlops LAMONT, 1949; Schrank, pp. 115, 119.

non 1970 Calymene frontosa LINDSTRÖM, 1885; Schrank, p. 116, pl. 1, figs. 1, 2.

LECTOTYPE. Here designated; a damaged but almost complete specimen which is enrolled; RM Ar6210; figured Lindström 1885, pl. 15, figs. 1-3 and here Pl. 3, figs. 1, 2, 4.

TYPE STRATUM AND TYPE LOCALITY. Lower (?) Visby Beds (topmost Llandovery in age), Visby, Gotland.

PARALECTOTYPES. Two damaged complete specimens which are both enrolled, RM Ar6211, figured Lindström 1885, pl. 15, fig. 4; RM Ar6212.

ADDITIONAL MATERIAL. Twenty six damaged, almost complete specimens, RM Ar27072, RM Ar27066, RM Ar27067, RM Ar42807, RM Ar42808, RM Ar27037-041, RM Ar27043, RM Ar27044, RM Ar27049-51, RM Ar47000, RM Ar47003-012, RM Ar47845; one hypostome, RM Ar27054; a pygidium with several attached thoracic segments, RM Ar27053.

DIAGNOSIS. Species of Calymene with the following characteristics: Glabella protrudes well above fixed cheek in lateral profile. Axial furrow wide (tr.) around lobe 1p, very wide in front of genal buttress. Preglabellar furrow is a fairly long, deep trough. Anterior border is a very steeply sloping, wall-like structure. Inner, anterior part of fixed cheek produced into a subconical projection. Lateral and posterior border furrows are very narrow. Thorax has twelve segments. Large, perforate, widely-spaced tubercules present on glabella and inner part of fixed cheek.

DESCRIPTION. Cephalic outline is generally subtriangular. Glabella is just longer than wide, bell-shaped in outline, projects marginally in front of fixed cheek. Occipital ring gently convex in profile, about twice as wide at median line than at axial furrow where it is axe-shaped; outer margin of axe-shaped extremity is almost straight (exs.), anterior corner is quite sharply angled and drawn forwards somewhat. Occipital furrow narrow behind central glabellar area, widens and deepens behind suboval to subcircular lateral lobe 1p which is about $\frac{1}{4}$ as wide as glabella, quite strongly inflated and separated from median lobe by shallow furrow. Lateral furrow 1p very deep at axial furrow, runs inward and backward to divide into anterior and posterior branches between which the glabellar side is gently swollen and sometimes developed into a small intermediate lobe. Lateral lobe 2p is joined to adaxially pointed genal buttress to form bridge over axial furrow. Furrow 2p transversely directed. Lobe 3p about one-third the size of lobe 2p, confined by short (tr.) 3p furrow.

Side of frontal lobe runs forward and slightly inward, anterolateral margin is well rounded, anterior margin very weakly convex forwards. Anterior face of frontal lobe slopes vertically to and is fractionally undercut by preglabellar furrow. In lateral view dorsal surface of glabella stands strongly above fixed cheek, it falls gently from occipital furrow to lobe 2p after which it descends progressively more steeply to frontal lobe.

Beside occipital ring the shallow axial furrow trends forward and outward to posterior border furrow then forward and inward to lobe 1p where it is narrowest (tr.), as it progresses forwards around this lobe it becomes gradually deeper and wider. In front of lobe 2p axial furrow is very deep, about twice as wide here as beside outermost margin of lobe 1p, its abaxial wall is vertical or slightly undercuts the fixed cheek. There is a small anterior pit below frontal lobe on inner side of the base of the axial furrow. Preglabellar furrow as deep and as wide (sag.) or slightly wider than axial furrow in front of lobe 2p; medially the preglabellar furrow is somewhat shallower than opposite (exs.) axial furrow due to a broad (tr.) rise of the floor of the furrow. Anterior side of preglabellar furrow slopes at first forwards and upwards, then vertically to dorsal surface of anterior border which is convex and slightly wider (exs.) near facial suture than sagittally. Dorsal surface of anterior border reaches about half-way up anterior face of frontal lobe (see frontal views). Outer side of anterior border descends steeply and marginally backwards to rostral suture, in frontal view it is considerably wider near facial suture than at median line. In front of glabella the anterior margin of cranidium is approximately straight (tr.) or very gently arched forwards, abaxially it bends quite sharply backwards towards fixed cheek.

Posterior border expands abaxially from fulcrum. Posterior border furrow narrow and deep from axial furrow to a point just short of facial suture. Postoccular part of fixed cheek is subtriangular in shape in dorsal view, bends strongly downward and outward. In frontal view fixed cheek is convex and slopes downward and outward between genal buttress and palpebral lobe. Inner, anterior corner of fixed cheek is pointed and drawn acutely forward in the form of a subconical projection which reaches towards anterior border. Furrow between this projection and anterior border is very narrow (exs.) and deep; the base of the furrow has a central crest either side of which it falls steeply down to the preglabellar furrow and facial suture.

Anterior branch of facial suture trends forwards and slightly inwards to anterior margin, then runs horizontally across anterior facing side of border to meet rostral suture. Posterior branch is directed transversely for a short distance from eye, then turns sharply backwards to cross lateral border furrow, thereafter running almost exsagittally before finally swinging outwards again to cut genal angle. Palpebral lobe is rather small - about as long as or slightly shorter (exs.) than lobe 2p, confined by shallow palpebral furrow, centred opposite (tr.) anterior part or margin of lobe 2p, is narrow and gently convex (tr.), projects outwards from fixed cheek. Eye lenses not observed but void between eye socle on free cheek and palpebral lobe is very small. Eye socle composed of two parts: an uppermost extremely narrow rim which is separated from a parallel, broader, lower platform by a faint, narrow furrow. This broader platform is in turn demarcated from the very steeply sloping main field of the free cheek by a break in slope. Lateral border furrow is a very narrow, deep slit which shallows near posterior facial suture. Dorsal surface of lateral border turns sharply over and passes into the wider, outer and downward facing side. On lateral border near junction with its doublure there is a narrow, tubercle-free strip of cuticle which continues onto the inner arc of the border sector of rostral plate. On outer side of this strip there is an exceedingly fine ridge which also continues anteriorly onto rostral plate.

Rostral suture broadly arched; connective suture abaxially convex; inner arc of border sector somewhat more convex than rostral suture. Hypostome is as long (exs.) at posterior spine as it is wide between (tr.) anterior wings. Anterior margin moderately arched. Anterior border narrow (sag.), reflexed ventrally. Anterior wing quite large with distinctly impressed anterior pit. Inside lateral notch, lateral border is tightly convex (tr.). Behind posterior wing border is expanded into very long, flat spine. Inner margins of the two posterior spines diverge only very weakly. Anterior lobe about four times as long as posterior lobe, bears a centrally positioned, ventrally directed projection. Ovate, slightly convex maculae joined by very weak median furrow.

Thorax contains twelve segments. Morphology of axial ring as for occipital ring except anterior corner of blunt extremity tends to be more drawn forwards and more sharply pointed. Anterior and posterior pleural bands are flat topped, of about the same height (see lateral views), at the fulcrum of about equal length (exs.), and separated by a narrow distinctly impressed pleural furrow.

Pygidial axis about two fifths to one half as wide as pygidium, tapers fairly strongly posteriorly, has six axial rings, at least first four of which are confined by a complete ring furrow. Small terminal axial piece has a rounded or somewhat medially pointed posterior outline. Pleural region descends very steeply away from axial furrow. Exact nature of pleural and interpleural furrows uncertain as nearly all specimens are tightly enrolled and many have been badly abraded.

There are five pleural furrows which are more deeply impressed and slightly longer than the interpleurals. Postaxial sector falls vertically from terminal axial piece.

Glabella, dorsal surface of anterior border, inner part of fixed and free cheek all ornamented with large, widely-spaced tubercules each of which is perforate. All sizes of tubercules down to very fine pustules are scattered in between these larger tubercules. Lateral border and border sector of rostral plate adorned with rounded, closely-set, medium and small sized tubercules together with fine pustules. All cranidial furrows devoid of ornament. Ornamentation on thorax and pygidium has been largely effaced but scattered tubercules observed on axial rings, pleurae, pygidial axis and pleural region, and fine pustules on pleural facets.

DISCUSSION. The abundant, excellently preserved material of Calymene frontosa has demanded a more lengthy description than usual. Lindström's original specimens have been examined and one of them (RM Ar6210) refigured for the first time. Schrank (1970) has revised this taxon on the basis of two specimens, one from Gotland, the other from a glacial erratic, but these are here considered to belong to a species which is distinct from Calymene frontosa (see discussion of Calymene sp. nov.?).

The horizon and locality information on the label accompanying the lectotype reads "Silurian, Visby, Gotland". Lindström (1885, p. 70) simply recorded the species from the Visby Marl. The Visby Beds are now split into a Lower and Upper division, both of which outcrop at Visby, with the boundary between the two being taken as approximately equivalent to the Llandovery - Wenlock boundary. I am uncertain as to which of these horizons yielded the type specimen and none of the other specimens at hand give more precise details as to the age of the species. Hede (1921, p. 99), however, records the species only from the Lower Visby Marls and this Lower division is therefore tentatively taken as the type stratum.

Calymene frontosa is one of two members of the genus I am aware of which have twelve, instead of the normal complement of thirteen thoracic segments. The other is C. puellaris Reed, 1920 from the middle Ludlovian, but the two species show innumerable differences and are not thought to be closely related. This ability to 'lose' a thoracic segment does not seem peculiar to any one species group, though it is a fairly rare phenomenon. Other interesting features which help characterize C. frontosa include: the deep and wide preglabellar furrow; deep and fairly wide axial furrow in front of lobe 2p; relatively high, vertically directed anterior border; the pointed, projecting anterior corner to the fixed cheek; a small palpebral lobe, nature of the eye socle, and the possession of a palpebral furrow; the deep posterior and lateral border furrows; a narrow strip of cuticle which is devoid of tubercules all around the anterior and lateral margins of the cephalic region; the unusually long, weakly diverging posterior spines of the hypostome; the form of the abaxial extremity of each axial ring; the type of cranidial ornamentation.

The cephalic outline of frontosa is typically subtriangular but in one specimen (RM Ar47000) it is much more semicircular. This same specimen also shows a relatively lower anterior border(see frontal view) but I have preferred to consider it a more extreme member of the frontosa population. The hypostome of the lectotype has been prepared (projection on anterior lobe just visible in frontal view) but was impossible to photograph fully on account of the partly enrolled nature of the specimen. It is 'identical' to that of the isolated hypostome which is figured (RM Ar27054).

There can be few species of Calymene which are so easily distinguished from each other than C. frontosa and C. laevis Lindström, 1885 yet in certain features they can be closely compared. These features are: the narrow (exs.) posterior border furrow of the cranidium, the rather blunt distal margin to each axial ring (though in laevis the anterior margin is not so pointed), the thoracic pleurae - flat-topped with the anterior and posterior pleural bands of equal height and of about equal length (exs.) at the fulcrum, and the narrow, slit-like pleural furrow. The form of the pleurae in particular provides a connection between C. frontosa (and associated species) and C. laevis, and at the same time contrasts markedly with the type seen in the group of species centred around C. blumenbachii and C. clavicula, which are discussed below.

Calymene carlops Lamont, 1949 and Calymene sp. nov.? are both strongly allied to frontosa and carlops may even be conspecific (see discussions of both species below). Schmidt (1894) has recorded frontosa from Estonia but only the specimen he depicted on pl. 2, figs. 4,4a seems to reasonably match the Gotland species (Schrank 1970, p. 116). More recently Kaljo (1970, p. 154) has listed, but not described, C. frontosa from the Adavere Stage (= upper middle and late Llandovery in age) of Estonia. I have examined calymenids (PMO 42726, PMO 91110) from Norway which are about late Llandovery to early Wenlock in age and which also belong in the frontosa group of species.

C. frontosa shows an interesting link with both Diacalymene and Papillicalymene in the form of the inner, anterior corner of the fixed cheek. Like C. frontosa, species of Diacalymene typically have a somewhat projecting fixed cheek, though in frontosa the ancestral condition has become more strongly developed. The 4p buttress which occurs in Papillicalymene is a similar structure to the subconical cheek of frontosa (see Whittington, 1971, pl. 85, fig. 6, pl. 86, fig. 16) but in the former it is directed more inwards. The likeness of the anterior border of frontosa to that of Papillicalymene species has been commented on (above and Schrank 1970, p. 142).

OCCURRENCE. (Lower?) Visby Beds of the Visby area, Gotland. Recorded, but not described from the Estonian Llandovery. Possibly present in the Telychian of the Pentland Hills, Scotland (see discussion of C. carlops.).

Calymene carlops Lamont, 1949

Plate 7, figs. 1-7.

? 1885 Calymmene frontosa n.; Lindström, p. 69, pl. 15, figs. 1-4.

1949 Calymene carlops sp. nov.; Lamont, p. 319, pl. 18, figs. 13-19.

1970 Calymene carlops LAMONT, 1949; Schrank, pp. 115, 119.

SYNTYPES. Internal mould of an incomplete cranidium, RSM 1956. 15. 52 (formerly Lamont Collection No. 34), figured Lamont 1949, pl. 18, figs. 13, 14, and herein Pl. 7 , figs. 3,4,6,7; internal mould of a pygidium, RSM 1956. 15. 53 (formerly Lamont Collection No. 35), figured Lamont 1949, pl. 18, fig. 17.

TYPE STRATUM AND TYPE LOCALITY. "Plectodonta aff. canastonensis siltstones" (after Lamont 1949, p.320), Deerhope, north of Carlops, N Esk Inlier, Pentland Hills, Scotland. These siltstones are thought to be of Upper Llandovery age (Cocks et al. 1971, fig. 6).

ADDITIONAL MATERIAL. a) specimens used by Lamont:- Three internal moulds of incomplete cranidia which were figured by Lamont in 1949, pl. 18, figs. 15, 16 and 18, respectively: G I G Colln. unnumbered, RSM 1876. 42. 6A - John Henderson Colln., RSM 1876. 42. 6B - John Henderson Colln.. One internal mould of a pygidium which was figured by Lamont 1949, pl. 18, fig. 19. RSM 1876. 42. 6C - John Henderson Colln.

b) specimens on loan from Mr. J. Tipper, Grant Institute of Geology, Edinburgh:- Internal moulds of three pygidia, Nos. 104, 106, 107a; one very small internal mould of a cranidium, 107c; one internal mould of a cranidium and its counterpart, 107d.

DISCUSSION. This species was founded on the basis of several internal mould specimens. Lamont believed C. carlops most akin to C. frontosa but contended his taxon differed by having a less tapering and longer frontal glabellar lobe and finer surface tubercules. Of Lamont's original specimens only one syntype cranidium (RSM 1956. 15. 52) is well enough preserved to assess the form of the frontal lobe. This lobe seems identical in shape with that of C. frontosa, and though it protrudes a little further in front of the fixed cheek than in the Gotland taxon, this difference alone does not appear to merit specific distinction. Schrank (1970, p. 119) considered carlops to have smaller lateral glabellar lobes than frontosa but I cannot uphold this conclusion.

It is difficult to compare the traces of ornament left on the internal moulds of carlops with the well preserved ornament on the frontosa specimens, but a cast of the only external mould cranidium I have available (J. Tipper Colln. No. 107d) shows it to be the same in both species. Also the form of the glabella (and its frontal lobe) and fixed cheek in this cranidium are indistinguishable from that of frontosa. The following differences are nevertheless apparent: the Pentlands specimen has a shorter preglebellar furrow, a relatively higher anterior border and a slightly longer palpebral lobe. A more adequate sample of carlops is required before these differences can be meaningfully interpreted. Meanwhile I have questionably retained it as a species distinct from frontosa.

OCCURRENCE. Upper Llandovery, Wetherlaw Linn and Deerhope Burn, N Esk Inlier, Pentland Hills, Scotland.

Calymene sp. nov.?

Plate 5, figs. 1-9; Plate 6, figs. 1-8.

? 1949 Calymene carlops sp. nov.; Lamont, p. 319.

1970 Calymene frontosa LINDSTRÖM, 1885; Schrank, p. 116, pl. 1, figs. 1, 2.

MATERIAL. Twelve damaged, almost complete specimens, RM Ar27042, RM Ar27046-048, RM Ar27052, RM Ar27058, RM Ar27060, RM Ar27071, RM Ar27073, RM Ar47001, RM Ar47013, RM Ar47014; eight cranidia, RM Ar27061 - 064, RM Ar27068, RM Ar27069, RM Ar27045, RM Ar47002; two cephala and two cranidia with several attached thoracic segments, RM Ar47861 - 862, RM Ar47865 - 866.

OCCURRENCE. Visby Beds (which are not divided into 'Lower' and 'Upper' on any of the labels accompanying the specimens), from Visby, Visby Hamn, and Visby Norderstrand, Gotland.

Specimens RM Ar47861 - 862 and RM Ar47865 - 866 are labelled as coming from "Hablingbo" (= Hemse Beds). It seems likely that this information is incorrect (see 'type stratum and type locality' of Calymene eximia sp. nov.).

DISCUSSION. In the (Lower ?) Visby Beds of Gotland there are many complete specimens of a Calymene which at first glance would be referred to C. frontosa. Closer examination reveals that these individuals have thirteen, not twelve, thoracic segments. They also display other features which differentiate them from the specimens with twelve segments. These characters include: a glabella which projects more strongly above the fixed cheek (compare lateral view of RM Ar27042 with RM Ar27038 or RM Ar27048 with RM Ar47003); an even deeper lateral border furrow; a much wider lateral border which is less tightly convex near the connective suture (compare frontal and lateral views of RM Ar27042 with RM Ar27038, and frontal, lateral and ventral - oblique views of RM Ar27048 with RM Ar47003); a border sector of the rostral plate which slopes more steeply downwards - and is thus more completely visible in frontal view (compare RM Ar27042 with RM Ar27038); a higher anterior border - the dorsal surface of which reaches farther up, if not above, the anterior face of the frontal glabellar lobe (compare frontal views of RM Ar27042 with RM Ar27038 or RM Ar27048 with RM Ar47003). In addition the specimens with thirteen segments have a pygidium with extremely deep pleural furrows (accounting for the fact that some may have been deepened during previous preparation) and a distinct medial ridge on the postaxial sector; these characters may also prove to be different (pygidium of the specimens with twelve segments is imperfectly known; see description of C. frontosa and compare lectotype with RM Ar27060).

As the horizon and locality details for both groups of specimens are the same, the above distinctions can be accounted for in at least three different ways: They may be an expression of intraspecific variation, interspecific variation , or sexual dimorphism. A difference in more than one character suggests one of the latter two alternatives is the most likely explanation, and I shall regard the specimens with thirteen segments as a different species from those with twelve (C. frontosa Lindström being here restricted to contain only the latter).

Formal recognition of the second species from Visby, (= Calymene sp. nov.? of this paper), which is based on well preserved specimens, is unfortunately dependant on a more complete knowledge of the morphology of C. carlops. The only reasonably preserved cranidium of carlops was, like the second Visby species, said to differ (in part) from frontosa by its relatively higher anterior border, so that carlops may prove to be conspecific with Calymene sp. nov.? rather than with C. frontosa. For this reason the synonymy of carlops has been treated with caution.

The two specimens assigned to C. frontosa by Schrank (1970, pl. 1, figs. 1, 2) are incomplete, having at most only three thoracic segments, but on the basis of their cephalic morphology they can be referred to Calymene sp. nov.? and not frontosa.

Calymene eximia sp. nov.

Plate 8, figs. 1-7.

DERIVATION OF THE NAME. From the Latin, eximius, uncommon; the species is known only from the holotype.

HOLOTYPE. A well preserved cephalon with the remains of at least four thoracic segments; RM Ar47864; Pl. 8, figs. 1-7.

TYPE STRATUM AND TYPE LOCALITY. The locality information on the holotype reads "Gotland, Hablingbo"; if this is correct, it comes from the Hemse Beds (= lower and middle Ludlow in age). There are several other specimens (RM Ar47859 - 863, RM Ar47865 - 869) in the same box and with the same locality information as the holotype; these specimens can be referred to at least three other species. Two of these species (Calymene tuberculosa and Calymene sp. nov.? (of this paper)) are found at much lower horizons, and it seems probable this box of specimens has at some time been contaminated. The type stratum and type locality given above for Calymene eximia sp. nov. is therefore open to some doubt.

ADDITIONAL MATERIAL. None known.

DIFFERENTIAL DIAGNOSIS. Species of Calymene related to C. frontosa but differing mainly in having a glabella very much longer than its fixed cheek, considerably narrower (tr.) axial furrow, and substantially shorter (sag. & exs.) preglabellar furrow.

DESCRIPTION. Cephalon not quite twice as wide as long, subtriangular in outline. Glabella scarcely as wide as it is long, bell-shaped in outline, projects anteriorly well beyond the fixed cheeks. Occipital ring gently convex (sag.), is axe-shaped at axial furrow as in C. frontosa, slightly narrower (tr.)than glabellar width. Occipital furrow narrow (sag. & exs.), much deeper behind lobe 1p than medially. Furrow 1p very narrow and deep between first two lateral lobes, widens considerably as it reaches central glabellar lobe which is very faintly swollen at this point; shallow depression continues over inner neck of lobe 1p to occipital furrow. Subcircular lobe 2p joined to genal buttress. Node-like 3p lobe present on dorsolateral glabellar margin. Lobe 4p very weakly inflated; 4p furrow very shallow. Frontal glabellar lobe slightly less than four times as wide as long, has well rounded anterolateral margins and a blunt anterior margin, slopes steeply to preglabellar furrow.

Axial furrow very narrow and deep around lobe 1p, slightly wider (though still deep) at furrow 1p and in front of lobe 2p. Shallow anterior pit sited on inner side of axial furrow below posterior part of frontal lobe. Preglabellar furrow an extremely narrow (sag. & exs.), deep slit which undercuts frontal glabellar lobe. Anterior slope of preglabellar furrow curves very steeply forwards and upwards and passes into convex (sag.), dorsal surface of anterior border. Anterior margin of cranidium very weakly arched forwards. Morphology of fixed and free cheek as in Calymene sp. nov.? (of this paper) except anterior part of fixed cheek a little less sharply pointed.

Rostral suture very broadly arcuate; connective suture almost straight; inner arc of border sector of rostral plate more strongly arched than rostral suture. Border sector four and a half times as wide as long. Hypostome like that of C. frontosa or Calymene sp. nov.? except inner margins of posterior spines diverge slightly more strongly and posterior spines are marginally narrower (tr.).

Morphology of thoracic axial rings the same as occipital ring. Pleurae are flat-topped; pleural furrow deeply incised. Number of thoracic segments and pygidium unknown.

Ornament much as in C. frontosa or Calymene sp. nov.? except tubercles on border sector of rostral plate cover the whole sector - there is no tubercle-free zone running parallel with the inner arc. This zone is present on free cheek but pinches out near connective suture.

DISCUSSION. A reluctance to erect this new species on the basis of one cephalon was outweighed by the excellently preserved nature of the specimen, which can be accurately compared with specimens of the same size belonging to other, closely allied taxa. C. eximia is undoubtedly related to the C. frontosa group of species on account of the form of its thoracic pleurae, occipital and axial rings, fixed cheek, palpebral lobe and eye socle, free cheek, and the general morphology of its hypostome. It is easily distinguished from all other species of the C. frontosa type in having a glabella very much longer than the fixed cheek, a substantially narrower axial furrow - especially in front of lateral lobe 2p, and an extremely short preglabellar furrow - which is considerably shorter than the anterior border. Therefore the glabella in C. eximia almost completely occupies that central portion of the cranidium which is bounded abaxially by the inner margin of the fixed cheek, and anteriorly by the anterior side of the preglabellar furrow; in the other species of the frontosa group it does not. Differences in the hypostome and ornament of the rostral plate further distinguish C. eximia from C. frontosa and Calymene sp. nov.? (see description).

Schrank (1970, p. 119) described a cranidium from the Mulde Beds (= upper Wenlock) of Gotland which he referred to Calymene sp. aff. frontosa. This specimen mainly differs from frontosa (and Calymene sp. nov.?) by having a wider frontal lobe and correspondingly narrower axial furrow. The axial furrow of C. aff. frontosa is therefore very much like that of C. eximia, though the two cranidia are not considered conspecific as the preglabellar furrow of the Wenlock cranidium is much longer, and the outer part of the facial suture almost straight (see Schrank p. 119-20). The axial furrow in front of lobe 2p is rather wide in both C. frontosa and Calymene sp. nov.?, but the width seems rather more variable and sometimes a little narrower in the latter species (compare RM Ar27042 and RM Ar27038). C. aff. frontosa of Schrank may represent an intermediate taxon - both in morphology and stratigraphy - in a line of descent from Calymene sp. nov.? to C. eximia.

OCCURRENCE. Known only from the type stratum and type locality.

Calymene hadyardensis Lamont, 1949

Plate 7, figs. 9, 12-14.

1949 Calymene hadyardensis sp. nov.; Lamont, p. 316, pl. 18, figs. 9 - 12, ? fig. 8.

1970 Calymene hadyardensis LAMONT, 1949; Schrank, pp. 116, 131.

HOLOTYPE. A poorly preserved internal mould of a complete specimen; G I G Colln. No. 1521; figured Lamont 1949, pl. 18, figs. 9 - 12, and here Pl. 7, figs. 9, 12-14.

TYPE STRATUM AND TYPE LOCALITY. The original data reads "Bargany Pond Burn Group (Lower Gala), N side of Hadyard Hill, S W of Dailly", Girvan district, Scotland (Lamont 1949, p. 318). The rocks on the N side of Hadyard Hill are of Upper Llandovery age; in particular they appear to belong to the Drumyork Flags which straddle the griestoniensis and crenulata zones of the upper Telychian (see Cocks and Toghill 1973, pp. 230, 238).

PARATYPE. A disarticulated specimen which has the cuticle remaining on the front of the glabella, anterior border, and part of the pygidium; RSM 1956. 15. 54 (formerly Lamont Colln., No. 33); figured Lamont 1949, pl. 18, fig. 8, and here Pl. 7 , figs.8, 10, 11, 15.

The original data for the horizon and locality of this specimen reads: "Penkill Group (Lower Gala), Penwhapple gorge, near Penkill Castle", Girvan district, Scotland (Lamont 1949, p. 318). The strata near Penkill Castle belong to either the Penkill Formation or Protovirgularia Grits in the sense of Cocks and Toghill (1973, pp. 227, 228). From the discussion which these authors present of the lithology and outcrops of the two groups of rocks, it seems more likely the paratype was obtained from the Penkill Formation (= turriculatus zone of the Telychian). But Cocks and Toghill (1973, fig. 9) do not indicate a shelly horizon within either the Penkill Formation or Protovirgularia Grits, and there is therefore the possibility that the paratype was obtained from either the Lower Camregan Grits (= uppermost Fronian) of Wood Burn Formation (= lowermost Telychian), both of which outcrop in Penwhapple Burn, though a little farther upstream (Cocks & Toghill 1973, fig. 9).

OTHER MATERIAL. None known.

DESCRIPTION (of the holotype). Glabella is bell-shaped. There appears to be at least three lateral glabellar lobes and 2p lobe is joined to a genal buttress. Anterior part of fixed cheek quite strongly overhangs abaxial continuation of the preglabellar furrow though this overhang is to some extent the result of deformation. Free cheek descends very steeply from facial suture but again this can in part be accounted for by deformation. Preglabellar furrow is moderately deep and, when the dorsal surface of the glabella is oriented horizontally, the anterior border is upturned at an angle of about forty-five degrees. Thorax has thirteen segments; the extremities of the better preserved axial rings trend forwards and their anterior corners are somewhat pointed. In posterior view the pygidium has a generally triangular appearance; axis has at least five rings and tapers sharply posteriorly. Pleural region has five pleural furrows.

DISCUSSION. C. hadyardensis was established on the basis of two specimens, the holotype and a paratype, and no other specimen has since been referred to the species. As far as can be determined from the holotype, the general form of the anterior part of the fixed cheek, the lateral portions of the axial rings, and the pygidium all suggest C. hadyardensis is related to C. frontosa, Calymene sp. nov.?, and C. eximia. But the holotype is for the most part very poorly preserved, and it is impossible to base a diagnosis of the species on this specimen.

The paratype is much better preserved, but is not from the type stratum or type locality; after further preparation it has turned out to be a species which is closely related to Calymene eximia sp. nov., but differs from that species in having a more posteriorly sited eye and exsagittally wider (after allowing for its internal mould condition) posterior border furrow. The strongly tapering nature of the pygidial axis in the paratype is like that of the holotype of hadyardensis, but other taxa (for example Calymene sp. nov.?)also exhibit this feature. The preservational shortcomings of the holotype militate against further close comparison with the paratype and it is not possible to say with conviction that the two specimens are conspecific. C. hadyardensis can only be made into a useful taxonomic unit by the collection of better preserved topotype material. This is likely to prove most difficult and it may be best to regard the species as a nomen dubium.

Calymene laevis Lindström, 1885

Plate 9, figs. 1-7; Plate 10, figs. 1-3.

1885 Calymmene laevis n.; Lindström, p. 68, pl. 16, figs. 5-7.

? 1928 Calymmene laevis LDSTR.; Kummerow, p. 9.

1970 Calymene laevis Lindström, 1885; Schrank, p. 116.

LECTOTYPE. Here designated; slightly damaged, complete,enrolled individual; RM Ar6334; figured Lindström 1885, pl. 16, figs. 5-7 and herein Pl. 9, figs. 1, 3, 5-7.

TYPE STRATUM AND TYPE LOCALITY. Slite Beds (= middle Wenlock), Västergarn, Gotland.

ADDITIONAL MATERIAL. Three almost complete enrolled individuals, RM Ar27233, RM Ar27234a, RM Ar27234b; three incomplete cranidia, all SGU unnumbered, H. Hedstrom (27), 11.6.1920.

DIAGNOSIS. Calymene with very narrow cranidial axial furrow. Glabella (and its lobes) is depressed, transversely and sagittally it forms part of a smoothly continuous cephalic outline. Palpebral lobes centred opposite anterior part of lobe 2p.

DESCRIPTION. Outline of cephalon is semicircular; enrolled specimens are remarkably spherical. Glabella is about 1.1 times as long as wide, bell-shaped in outline - its sides converging from the most abaxial outer side of lobe 1p to lobe 2p but between furrow 2p and preglabellar furrow they are subparallel. Occipital ring fractionally narrower (tr.) than glabella, uniformly long behind central glabella area, quickly shortens behind lobe 1p to axial furrow, in profile it is flat. Occipital furrow a narrow, shallow, transversely directed nick in the median region, deeper but still very narrow abaxially. Subquadrate lateral lobe 1p is about one third as wide as and one third as long as glabella, joined to median lobe by a narrow neck. Furrow 1p very narrow between 1p and 2p lobes, bifurcates adaxially and within this fork the median glabellar lobe is moderately swollen (RM Ar27234a) or is augmented with a discrete intermediate lobe (holotype). Lateral lobe 2p subcircular or somewhat elongate (outwards and forwards), about half the size of lobe 1p, confined on its inner side by almost imperceptible depression. Slit-like furrow 2p trends inwards and marginally backwards. Lobe 3p transversely elongate, confined anteriorly by short (tr.), narrow 3p furrow. In front of the latter a faint swelling indicates 4p lobe; no 4p furrow. Frontal lobe subrectangular, antero-lateral corner quite well rounded, about three and a half times as wide as long, anterior margin very weakly convex forwards, projects fractionally in front of fixed cheek, drops steeply into preglabellar furrow. In profile dorsal surface of glabella is unusually flat between occipital furrow and furrow 3p, thereafter only gently convex and gently sloping down to anterior margin of frontal lobe. Both transversely and sagittally the glabella profile is smoothly continuous with that of the rest of the cephalon and it protrudes little above the fixed cheeks.

Axial furrow V-shaped in outline around occipital ring, very narrow around lobe 1p, is interrupted at lobe 2p where truncate margin of that lobe is joined to fixed cheek, between furrow 2p and preglabellar furrow it is again a narrow trench. Preglabellar furrow about the same or marginally wider (sag. & exs.) than axial furrow, moderately deep, abruptly shallows abaxially at fixed cheek, anterior face slopes very steeply and runs smoothly at its upper surface into anterior border. Latter is moderately wide (sag.), in profile dorsal side turns fairly sharply over and passes into convex outer side which is of about the same width. Anterior margin is weakly arcuate forwards and upwards in dorsal and frontal aspects, respectively. Most dorsal point of anterior border does not reach above dorsal surface of frontal glabellar lobe.

Distance between axial furrow and fulcrum along posterior margin is about one quarter the width (tr.) of the occipital ring. Posterior border becomes less convex and wider (exs.) towards genal angle. Posterior border furrow narrow and U-shaped, fades out before reaching facial suture, is not quite as deep as axial or preglabellar furrows. Smooth, postoccular part of fixed cheek slopes progressively more steeply from axial furrow to genal angle. Palpebral lobe is a narrow (tr.), very gently inclined continuation of the fixed cheek, its outer margin is not broadly convex, but rather pointed, it is centred opposite anterior part of 2p lobe. Width (tr.) of preoccular fixed cheek about twice the length (sag.) of anterior border, slopes weakly forwards and downwards. Posterior branch of facial suture transversely directed from eye lobe, curves strongly backwards to cross exceedingly faint and shallow lateral border 'furrow', then turns more sharply backward before finally curving outwards to run to junction of posterior and lateral margins. Anterior branch almost straight, trends slightly inwards to anterior margin, curves sharply inwards from here to rostral suture.

Eye socle on free cheek is very narrow; mainfield of free cheek slopes steeply downward and passes almost without interruption into lateral border which curves strongly under and inward to meet strongly reflexed doublure.

Rostral suture parallels anterior margin. Border sector of rostral plate is gently arched. Connective suture weakly convex abaxially. Hypostome (known from one partly enrolled specimen (RM Ar27234b)) proved extremely difficult to prepare and photograph. It is similar to hypostomes of many other Calymene species. Anterior lobe of median body bears a very strongly developed, ventrally pointed projection. Maculae scarcely visible (though it is a small specimen). Posterior margin bifid.

Thorax contains thirteen segments. Axial ring widens slightly from median line (sag.) to axial furrow (exs.) where its outer margin is rather blunt and axe-shaped. Outside this blunt extremity, the axial furrow is V-shaped in outline, at the apex of the V it runs into the pleural furrow. In lateral profile axial ring is flat or at most very gently convex, articulating furrow is narrow and shallow but quite distinctly marked, articulating half-ring is of about the same relief as axial ring. Pleural furrow noticeably very narrow (exs.) and rille-like on dorsal side of pleuron (its course on articulating facet obscured by overlapping segments). At fulcrum posterior and anterior pleural bands are of equal height (see lateral view), almost equal length (exs.), and flat-topped. Posterior margins of posterior pleurae are more angular in outline than those of anterior pleurae.

Axis of pygidium tapers gradually, has six axial rings and is fairly convex (tr.). First five axial rings defined posteriorly by a complete ring furrow, though third to fifth furrows are poorly marked medially. Sixth ring furrow effaced sagittally. Terminal axial piece posteriorly rounded. Axial furrow V-shaped in outline beside first two axial rings. Pleural region falls steeply from axis. First pleural furrow more distinct than other four which on the holotype are feebly impressed though on another specimen (RM Ar27234a) they are slightly stronger. Interpleurals lacking adaxially, very feebly present on outer part of pleural region. Postaxial sector of pygidium not strongly protruberant, falls almost vertically from terminal axial piece.

Dorsal surface of cephalon appears almost completely smooth except for a few scattered small tubercles on inner anterior part of fixed cheek, outer parts of frontal glabellar lobe and more particularly the dorsal surface of anterior border. On lateral border of free cheek, border sector of rostral plate and outer side of anterior border the tubercles become more eliptical in shape and much more closely spaced. Thorax largely smooth except for a few small tubercles on lateral extremities and posterior margins of axial rings, and anterior and posterior pleural bands. Scattered tubercles on median posterior portion of pygidial axis and outer part of pleural region. Inner pleural region lacks tubercles.

DISCUSSION. This curious species has not been revised since it was founded in 1885. All of the material figured herein from the type locality of Västergarn was also seen by Lindström. C. laevis has several unusual characters, some of which are unexpected in a calymenid of middle Silurian age. Enrolled specimens are remarkably spherical in appearance. This is partly on account of the rather flat, depressed nature of the glabella which projects little above the fixed cheeks and in frontal view forms part of the evenly continuous dorsal outline of the cephalon; it is also due to the semicircular cephalic outline, and the generally smooth cuticular surface. There is no part of the cephalon, thorax or pygidium which stands prominently out from the rest of the exoskeleton. The narrow, scarcely inclined palpebral lobe, almost total lack of a lateral border furrow, non-inflated abaxial extremities to the axial rings, and flat-topped surface to the adaxial, dorsal surface of each pleuron all add to this effect. Also typical of C. laevis is the V-shaped outline of the axial furrow outside the blunt, axe-shaped extremity of each axial ring. Some of these features are also displayed by C. spectabilis and C. aquatica sp. nov.

Especially noticeable in C. laevis is the extremely narrow axial furrow beside the glabella. The narrowness of the furrow is, interestingly, reminiscent of that found in Liocalymene Raymond, 1916, a monotypic genus of uncertain derivation from the upper Llandovery of the central and eastern United States. Other characters such as the gentle transverse and sagittal convexity of the depressed glabella, smooth exoskeleton, form of the anterior border and the fixed cheek are not unalike in C. laevis and L. clintoni (Vanuxem, 1842). In L. clintoni the axial furrow beside the glabella (except most basal part of 1p lobe and occipital ring) is simply a narrow slit; the lateral glabellar and frontal lobes very closely approach (if not touch) the fixed cheek, but the 2p lobe is apparently not joined as an individual structure to a genal buttress (Whittington 1971, p. 473, pl. 89). In C. laevis the second glabellar lobe is definitely joined to the fixed cheek though there is only a very slight adaxial extension of the cheek at this point. It is important to distinguish between whether the glabellar lobe is coupled with or merely in contact with the fixed cheek. The anterior corner of the basal lobe in C. laevis is, in some specimens, touching but not conjugate with the fixed cheek, whereas the 2p glabellar lobe is both touching and conjugate (though it is not possible to determine - but it would seem unlikely - whether the axial furrow passes under this structure).

Apart from the apparent failure of lateral lobe 2p to be joined to the fixed cheek, L. clintoni is further differentiated from C. laevis by its unique pygidium, in which the pleural region has only one pleural and no interpleural furrows. The two species are here considered generically distinct but the Gotland material perhaps gives a useful clue as to the origin of Liocalymeme. If a Calymene species similar to

C. laevis or C. aquatica sp. nov. (see discussion of that species) had existed in late Ordovician or early Silurian times, it could have given rise to the North American genus by an effacement of the pleural and interpleural furrows and narrowing of the axial furrow outside the 1p, 3p and frontal glabellar lobes.

A discussion of C. laevis with C. aquatica sp. nov. and C. spectabilis is given below.

OCCURRENCE. In addition to the type stratum and type locality: from the Slite Beds at Bunge socken Farösund, Gotland. C. laevis was recorded, but not figured, from Silurian Baltic erratics (Kummerow, 1928, p. 9).

Calymene aff. C. laevis Lindström, 1885

Plate 14, figs. 4-8.

MATERIAL. Four incomplete cranidia, RM Ar27264, RM Ar27266 - 268; one almost complete specimen and its hypostome, RM Ar27222.

OCCURRENCE. Slite Beds from the Lokkrume Kanal and Eskelhem, Gotland.

DISCUSSION. This material from the Slite Beds represents a species similar to, but almost certainly different from, C. laevis. The cranidium is distinguished from that of C. laevis through its considerably more convex (sag. & tr.) glabella which has a less sinuous more gradually tapering (anteriorly) glabellar outline, and through its wider cranidial axial furrow. It differs most obviously from Calymene aquatica sp. nov. in its glabella outline.

The rostral plate is ornamented with flattened, rounded, scale-like tubercles over most of its outer surface, but near the inner arc of the border sector there are two parallel rows of very fine pustules. The hypostome is similar to that of C. laevis; it has a long, strongly developed median spine two thirds of the way along (sag.) the anterior lobe. The maculae are very weak, the posterior spines are only moderately long.

Through its more swollen less bell-shaped glabella, and its wider axial furrow, C. aff. laevis is leading towards C. spectabilis but Angelin's species has more posteriorly situated palpebral lobes and a lower, shorter (sag.) anterior border.

The form of the anterior border and more swollen glabella in C. aff. laevis is similar to that of C. neotuberculata Schrank, 1970 (see later). The latter species differs mainly in its narrower axial furrow - especially around lobe lp - and its much more distinct, coarser glabellar tubercles, but C. aff. laevis may represent a connection between the C. laevis and C. neotuberculata/C. blumenbachii groups of species.

Calymene aquatica sp. nov.

Plate 10, figs. 4-6; Plate 11, figs. 1-9.

DERIVATION OF THE NAME. From the Latin, aquaticus, living in or near water, alluding to the occurrence of the species in the Wallstena Kanal, the type locality.

HOLOTYPE. A cranidium; RM Ar27295; Pl. 11, figs.1-4.

TYPE STRATUM AND TYPE LOCALITY. Slite Beds (= middle Wenlock), Wallstena Kanal, Gotland.

ADDITIONAL MATERIAL. Five cranidia, RM Ar27284, RM Ar27289, RM Ar27300 - 301, RM Ar27305; one cephalon RM Ar27303; one cephalon with four attached thoracic segments, RM Ar27311; five damaged complete individuals, RM Ar27296 - 299, RM Ar27302.

DIFFERENTIAL DIAGNOSIS. Calymene similar to C. laevis Lindström, 1885, but differing mainly through a deeper preglabellar furrow and correspondingly higher anterior border, a more strongly bell-shaped glabella, a relatively wider cranidium, and a less well defined anterior branch of 1p furrow.

DISCUSSION. The Slite Beds of Gotland encompass a variety of carbonate and marly lithofacies and are more geographically widespread than any other part of the Island's Silurian succession. As a whole the Slite Beds are approximately coeval with the middle Wenlock (Cocks et al. 1971, fig. 9), but the age relations of all the constituent members is not yet clear (Martinsson 1962, p. 48). Martinsson (1962) found considerable differences between the ostracode faunas of these various members. The calymenid populations in the Slite Beds are of the C. laevis type, but they show substantial variation and to regard them as all belonging to one species would be an over - simplification of the picture. The type locality for C. laevis, Västergarn, is almost on the western coast of the outcrop; the new species erected here has not been found at Västergarn and occurs in localities towards the eastern side of the Island. The new species is probably slightly younger in age than C. laevis (see Martinsson 1967, p. 354 and p. 360).

In his discussion of C. laevis, Lindström (1885, p. 69) concluded by mentioning a variety met with at Slite which had a more curved (in outline) glabella and a wider cephalon. It is probable that

Lindströms variety is the same as C. aquatica sp. nov. The most constant (though perhaps not the most obvious) difference between C. aquatica and C. laevis is the anterior border which in the former is higher, reaching above the anterior margin of the frontal glabellar lobe, whereas in the latter it does not (see frontal and lateral profiles). Linked to this difference the pregleballar furrow of C. aquatica is much deeper, and in most specimens appears slightly longer (sag.) than in C. laevis. The glabellar outline of the new species narrows more sharply anteriorly on account of the less subrectangular glabella in front of lobe 2p, thus producing a more strongly bell-shaped outline than in C. laevis. Also, in aquatica the cranidium is wider relative to the length of glabella. There is some variation in the definition of an intermediate lobe at the inner end of furrow 1p in C. laevis (see description), but the anterior branch of furrow 1p is always quite sharply incised. The anterior branch is much weaker in C. aquatica, and though the side of the glabella is broadly convex posterior to this branch, there is no individual intermediate lobe. The overall inflation of the glabella varies somewhat in C. aquatica; it may be rather depressed (as in C. laevis) or more often it is moderately convex (sag. & tr.). The dorsal surface of the axial rings and pleurae in some specimens of C. aquatica are more rounded than in C. laevis.

C. aquatica has a glabellar outline and lateral furrow 1p which seem closer than those of C. laevis to those found in Liocalymene clintoni.

OCCURRENCE. Slite Beds, Gotland. The species is most abundant at the type locality but I have also seen specimens from Boge, Slite, and Dalhem.

Calymene spectabilis Angelin, 1854

Plate 12, figs. 1-8; Plate 13, figs. 1-10; Plate 14, figs. 1-3.

1854 Calymmene spectabilis. n. sp.; Angelin, p.28, pl. 19, fig. 5.

1885 Calymmene spectabilis ANGELIN; Lindström, p. 66.

non 1907 Calymmene spectabilis ANG.; Schmidt, p. 55, pl. 3, figs. 2-5.

1970 Calymene spectabilis ANGELIN, 1854; Schrank, p. 133, pl. 7, figs. 3-5.

LECTOTYPE. Designated Schrank 1970, p. 133; a damaged cephalon; RM Ar6208; figured Angelin 1854 (as part of a reconstruction) pl. 19, fig. 5, and Schrank 1970 pl. 7, figs. 4, 4a.

TYPE STRATUM AND TYPE LOCALITY. ? Klinteberg Limestone (= upper Wenlock to lower Ludlow), Djupvik, Eksta, Gotland. (after Schrank 1970, p. 133).

MATERIAL. Eight cranidia, RM Ar6205, RM Ar6207, RM Ar6208, RM Ar27902, RM Ar27911, RM Ar27913, RM Ar27947, RM Ar27898; three free cheeks, RM Ar27899 - 900, RM Ar27946; four pygidia, RM Ar6206, RM Ar27906, RM Ar27928, RM Ar31436; one poorly preserved cephalon together with its hypostome and several thoracic segments, RM Ar46996a-d; one disarticulated specimen and its hypostome, RM Ar46997a-b.

DIAGNOSIS. See Schrank 1970, p. 134.

DESCRIPTION. Glabella about 1.2 times as long as wide. Relatively small, subcircular basal lobe is less than one third as wide as glabella and extends only a short distance beyond lobe 2p. In front of latter glabella is subrectangular in outline. Furrow 1p is deep at axial furrow, runs inwards and backwards and divides into anterior and posterior branches between which there is a distinctly swollen intermediate lobe. Posterior branch is continued towards narrow (sag. & exs.), sharply incised occipital furrow as a very shallow depression. Subcircular lobe 2p is papillate and joined to genal buttress over axial furrow, separated from posteriorly narrowing median glabellar lobe by slight furrow. Transversely elongate lobe 3p is one third the size of lobe 2p. Lobe and furrow 4p also present. Outline of frontal glabellar lobe is subrectangular, its anterior margin is gently convex forwards. In profile surface of glabella projects well above fixed cheek, assumes a horizontal attitude from posterior margin of occipital ring to furrow 2p, descends gradually from here to anterior margin of frontal lobe.

Axial furrow deep and narrow around lobe 1p, is slightly wider next to lobe 3p, but narrows again at side of frontal lobe. In front of lobe 2p the abaxial wall of axial furrow is vertical and its upper margin meets the flat, forward and downward facing preoccular part of the fixed cheek to form a right-angle in transverse section. Preglabellar furrow moderately deep, trench-like, undercuts the frontal lobe, does not continue abaxially into lateral border furrow but runs posteriorly into axial furrow. Anterior border is very short (sag. & exs.), its upper surface turns quite sharply over and passes into the outer facing side which is considerably narrower medially than near facial suture (see frontal view), and which in profile continues the slope of the frontal glabellar lobe. Most dorsal point of anterior border does not reach as high as lowest part of frontal lobe (see frontal and lateral views). Anterior margin very weakly arched forward.

Postocular part of fixed cheek very wide (tr.) - about two and a half times as wide as it is long. Posterior border furrow is constantly narrow. Palpebral lobe centred opposite the posterior part of lobe 2p, its outer margin is distinctly pointed, slopes moderately to steeply inward and downward. Preoccular portion of fixed cheek very narrow (tr.) - only about as wide as (or even narrower than) lobe 2p. Posterior and anterior branches of facial suture are essentially as in C. laevis. Free cheek has very narrow eye socle; a wide, smooth inner region; very narrow, shallow lateral border furrow, and a broad lateral border.

Rostral plate unknown. Hypostome considerably wider (tr.) than long (sag.). Anterior border very narrow (sag.), slightly reflexed ventrally from anterior lobe. Anterior wing rather large with deep, slit-like pit which trends forwards and slightly inwards. Anterior lobe at least three times as long as posterior lobe, bears a very strongly developed projection. In one specimen (RM Ar46996b) this projection is hook-like, in another (RM Ar46997b) the posterior side of the projection is, initially, much more gently inclined and longer (sag.) before sloping very steeply down to the median furrow. The latter is deeply impressed near lateral border but almost lacking in median region. Maculae smooth, very weakly developed. Posterior lobe very mildly inflated (tr.), in one specimen (RM Ar46997b)almost flat. Posterior spine (RM Ar46997b) exceedingly short and narrow.

Isolated thoracic segments (RM Ar46997a; RM Ar46996a) appear to be like those of C. laevis. For example in the somewhat flat-topped form of the pleurae in which the anterior and posterior pleural bands are of equal height,and also the V-shaped outline of the axial furrow outside the blunt extremity of each axial ring.

Pygidium has eight axial rings. Anterior five rings confined posteriorly by a complete ring furrow, though third to fifth rings rather weak sagittally; sixth and seventh ring furrows only marked near axial furrow; very faint trace of eighth ring furrow on rounded (but somewhat pointed) postaxial sector. In lateral profile dorsal surface of axis is gently arched. Pleural region slopes steeply away from axial furrow, has six pleural furrows the last one of which forms the side of the weakly protruding postaxial sector. Interpleural much weaker than pleural furrows, best marked on outer half of pleural region, exceptionally faint or absent adaxially. Posterior face of postaxial sector is very steeply sloping.

Small to medium sized tubercles scattered over much of glabella, preocculal part of fixed cheek and anterior border. Lateral border of free cheek ornamented with longer, scale-like tubercles. Outer part of pygidial pleural region densely tuberculate; inner part less so.

DISCUSSION. The Lectotype of this species has recently been figured and is questionably recorded (Schrank 1970, p. 133, pl. 7, fig. 4) as coming from the Klinteberg Limestone at Eksta, Djupvik, Gotland. All the material I have is from the Hemse Beds (= lower and middle Ludlow), and most of this is from Östergarn on the eastern side of the Island. Schrank (1970, p. 116) has drawn attention to the relationship between C. spectabilis and C. laevis by combining them in his species group number six. This group is characterized by an anterior border which is rather low and has a slightly rounded upper edge which can be almost hidden by the projecting frontal glabellar lobe. The outer side of the anterior border is continuous with the slope of the glabellar outline in lateral profile. Other characters which ally the two species are the pointed outer margin of the palpebral lobe; the form of the thoracic axial rings, pleurae, and axial furrow (see descriptions); the failure of the preglabellar furrow to be distinctly continued abaxially in front of the fixed cheeks; the very narrow, weak lateral border furrow on the free cheek; the rather flat moderately sloping preocular part of the fixed cheek; the generally subquadrate outline of the glabella in front of lobe 2p, and the tendency for the lateral margin of the frontal glabellar lobe to trend fractionally forwards and outwards.

C. spectabilis differs from C. laevis in the following respects: The intermediate lobe at the inner end of lateral furrow 1p is more swollen and discrete from the median glabellar lobe, the cranidial axial furrow is wider and genal buttress better developed, the palpebral lobe is more posteriorly sited - opposite the posterior part of the lateral lobe 2p, the basal glabellar lobe is relatively smaller and thus the glabella somewhat less bell-shaped in outline, the glabella and its lateral lobes are more inflated, the dorsal surface of the anterior border is shorter (sag.), and the pygidium has more axial rings and pleural furrows. A further difference is that of absolute size - all the specimens of spectabilis are considerably larger than those of laevis and this should be kept in mind when considering the distinctions between the two species.

Another feature which is characteristic of C. spectabilis is the preoccular part of the fixed cheek which is rather narrow (tr.) - only about one quarter to one fifth as wide as the glabella at lateral lobe 2p (Schrank 1970, p. 134).

The two figured hypostomes are both from Östergarn and each is associated with parts of a cranidium and thorax which are best referred to C. spectabilis. The hypostomes agree in general morphology but the form of the projection on the anterior lobe is different (see description). Also the posterior lobe in the one specimen (RM Ar46997b) is noticeably more depressed. This suggests there may be more than one species represented by these two specimens. The posterior spines are not preserved in the one hypostome (RM Ar46996b) but in the other - which has only one spine remaining - it is exceptionally narrow (tr.) and short (exs.). For such relatively large specimens, the maculae on both hypostomes are inconspicuous.

When seen in frontal view the anterior borders of spectabilis and C. breviceps (see below) are alike in that both are much narrower sagittally than abaxially, but in dorsal view the border of spectabilis is longer (sag.), and many other differences divide the two species (compare descriptions).

It is worth noting that Angelin (1854, pl. 19, fig. 5) gives a most accurate depiction of the cranidium of C. spectabilis in his reconstruction of the species.

OCCURRENCE. Apart from the type stratum and type locality, I have seen specimens from the Hemse Beds at Östergarn, Fardhem, Ardre, and S of Grogarnshuvud, Gotland. Lindström (1885, p. 68) also records the species from the Hemse Beds at Petesvik and the Linda Klint, and also from the "Burgsvik and Grötlingbo sandstones"; I have been unable to substantiate the occurrence of spectabilis at these localities.

Kaljo (1970, p. 154) records C. spectabilis from the Kaugatuma and Ohesaare Stages (= approximately Downtonian in age; after Cocks et al., 1971, fig. 9) of the Estonian Silurian. As recognised by Schrank (1970), Schmidt's earlier reference (see synonymy) to this species is almost certainly in error. The glabella of the species figured by Schmidt is not unlike that of spectabilis but the eye is slightly more anteriorly placed and the anterior border much more prominent than in the Gotland taxon. Moreover the Estonian material has a rather deep furrow in front of the fixed cheek. C. conspicua Schmidt, 1894, C. ohhesaarensis Schmidt, 1894, and C. laevigata Schmidt, 1907 are all species from the late Silurian of Estonia which await revision. It is probable that the cranidia Schmidt referred to spectabilis belong to one of these species.

Calymene tuberculosa Dalman, 1827

Plate 15, figs. 1-11; Plate 16, figs. 1-11;
Plate 17, figs. 1-7; Plate 18, figs. 1, 2.

1827 Calymene Blumenbachii. var α, tuberculosa; Dalman, p. 227.

non 1848 Calymene tuberculosa, Salter; Salter, p.342, pl. 7, figs. 1-5

? 1854 Calymmene tuberculata. BRÜNN.; Angelin, p.29, pl. 19, fig. 5d.

1885 Calymmene tuberculosa DALMAN; Lindström, p.66, pl. 16, fig. 8.

? 1924 Calymene tuberculosa (Dalman); McLearn, p. 161, pl.16, figs. 3,4.

1936 C. tuberculosa Dalman; Shirley, p. 413.

1970 Calymene tuberculosa Dalman, 1827; Schrank, p.132, pl. 6, figs. 6, 7, pl. 7, figs. 1, 2.

1971 Calymene tuberculosa Dalman 1827; Whittington, p. 461.

NEOTYPE. Here designated; cephalon with the remains of three thoracic segments; RM Ar6230; figured Lindström 1885, pl. 16, fig. 8 and Schrank 1970, pl. 7, figs. 1, 1a.

TYPE STRATUM AND TYPE LOCALITY. Mulde Beds (= upper Wenlock - ellesae to lundgreni zones), Djupvik, Eksta , Gotland.

ADDITIONAL MATERIAL. More than 150 excellently preserved specimens, many of which are complete, enrolled individuals. The bulk of the material is housed in the Riksmuseet, Stockholm.

DIAGNOSIS. Species of Calymene with short anterior border, the dorsal surface of which is flat and narrow (sag. & exs.), the outer side of which rolls over in the form of a tightly convex rim. In frontal view rostral suture strongly arched, outer side of anterior border uniformly narrow. Abaxial portion of axial ring is conspicuously inflated in the form of a sharp, pointed node.

DESCRIPTION. Glabella longer than wide, bell shaped in outline, projects in front of fixed cheek. Occipital ring rather wide at median line, narrows quite sharply abaxially, is produced into swollen node at axial furrow, in lateral profile is moderately convex, slopes gently forward and downward. Occipital furrow shallowest behind central glabellar area, very deep posterior to lobe 1p. Latter is less than one third as wide as glabella, bounded adaxially by extremely shallow furrow. Lateral furrow 1p very deep, slightly bifurcates at median glabellar lobe but no conspicuous intermediate lobe within this fork. Papillate lateral lobe 2p meets genal buttress, confined adaxially by faint, narrow (tr.) depression. Furrow 2p transversely directed. Lobe 3p gently inflated, runs down glabellar side. Furrow 3p weak. Frontal lobe is rather swollen, has well rounded anterolateral margins, gently arched anterior margin. Glabellar profile (sag.) approximately horizontal from occipital furrow to lobe 2p, moderately vaulted from here to frontal lobe, thereafter descends steeply (sometimes vertically) to preglabellar furrow.

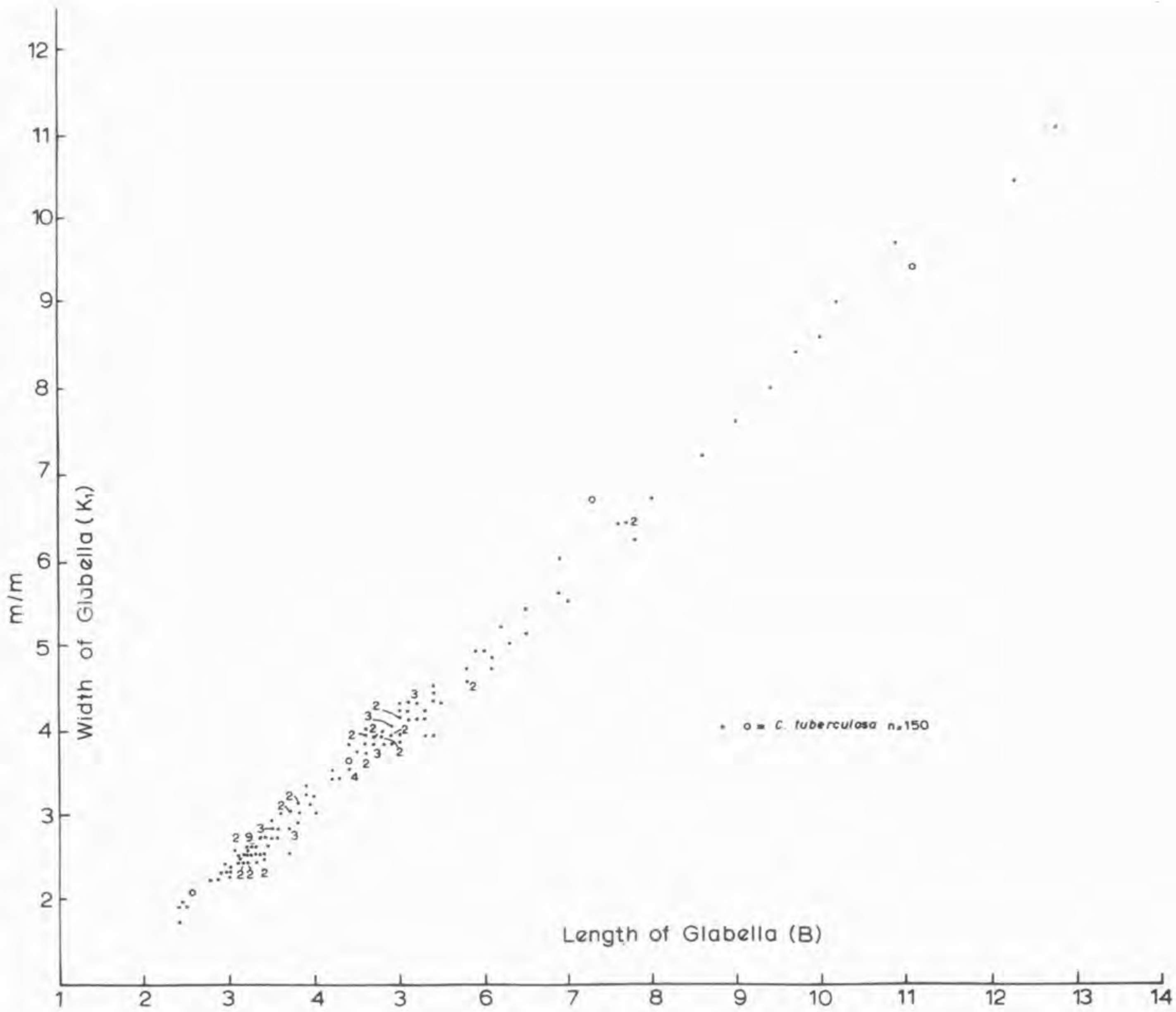
Axial furrow very deep beside basal glabellar lobe, forms a tunnel under lobe 2p and genal buttress, still very deep next to lobe 3p. Distinct anterior pit below posterior part of frontal lobe. Preglabellar furrow exceedingly shallow and constantly narrow. Anterior border is simple, low, tightly convex and very short (sag. & exs.), in lateral profile dorsal surface is rather flat and rolls over into narrow, downward and backward facing outer side. In dorsal view anterior margin gently convex forwards, in frontal view strongly arched downwards.

Posterior border furrow distinct, has much steeper posterior slope, widest at mid-length. Width of fixed cheek less than occipital ring. Highly inclined palpebral lobe centred opposite glabellar lobe 2p. Fixed cheek in front of palpebral lobe descends steeply. Posterior branch of facial suture runs at first transversely outward, before turning sharply backward to cross lateral border furrow, then fractionally more backward to meet posterior margin at acute angle; anterior branch curves forward and inward to anterior margin then turns sharply inward to join connective and rostral sutures. Free cheek bears a wide eye socle which is 'separated' from main field of cheek by broad furrow. Lateral border furrow well marked. Lateral border very wide, narrows slightly posteriorly, much of it is ventrally facing.

Rostral suture highly arched. Connective suture curves downward and inward, more sharply inward when nearing inner arc of border sector of rostral plate. Latter is shaped like an inverted U. Hypostome is wider than long. Anterior margin convex forward. Anterior border very narrow (sag. & exs.); anterior border furrow scarcely impressed. Large anterior wing has slit-like pit. Lateral border narrow (tr.) between anterior and posterior wings, broadens behind posterior wing into flat, fin-like projection. Posterior margin bifid and V-shaped. Posterior border furrow short (tr.) and shallow. Anterior lobe of median body augmented by a stout, subconical protruberance which is sited about two-thirds the length from anterior margin to median furrow. The latter is best marked abaxially, connected to two smooth highly inflated (less so on small specimens) ovate maculae. Crescent-shaped posterior lobe is about one third length of anterior lobe.

Thorax contains thirteen segments. Axial rings more or less uniformly narrow (sag. & exs.), produced into sharply pointed node at axial furrow, quite well rounded in section (sag.). Pleural furrow U-shaped, runs outward and forward onto articulating facet, finally swings backwards and fades out. Posterior pleural band considerably higher, wider (exs.), and more convex than anterior pleural band.

Pygidium about twice as wide as long, in dorsal view subtriangular in outline. Axis has six rings, each ring slightly swollen at axial furrow, swellings become less prominent towards posterior part of axis. Dorsal surface of axis is gently convex (tr.), slopes quite steeply on side of lateral axial swellings down to axial furrow. First five ring furrows complete, sixth incomplete. Short (sag.), posteriorly rounded terminal axial piece sometimes shows trace of seventh ring furrow medially. Inner part of pleural region slopes steeply, and outer part very steeply or vertically. There are five distinct pleural furrows which fail to reach lateral margin. Interpleural furrows are poorly


Width of Glabella (K₁)
m/m
Length of Glabella (B)
m/m
• o = C. tuberculosa n=150

TEXT-fig 1

defined and about as long as pleurals. Two ridges, one either side the axis, run exsagittally backward and downward from axial furrow near sixth axial ring; the outer sides of these ridges are vertically inclined and form the sides of the postaxial sector. Pygidial border rolled under, notched sagittally. Axial furrow weakest around terminal axial piece.

Glabella, fixed cheeks (excluding furrows) and anterior border have closely spaced medium-sized tubercles ranging down in size to fine granules. On border roll of free cheek and border sector of rostral plate tubercles are more flat topped. All around lateral margin of free cheek and inner arc of border sector (rostral plate) there is a row of very fine granules. Scattered fine tubercles on hypostome. Much of dorsal part of thorax apparently smooth, though some tubercles on anterior part of axial rings and axial nodes. Granules on articulating facets of pleurae; larger tubercles on lower parts of posteriorly bounding rims of articulating facets - which are the areas that are in contact with lateral margin of cephalon during enrollment. Most of pygidium covered with small to medium sized tubercles.

ONTOGENY. More than 150 specimens of this species have been measured. From a plot of glabellar length (variate B) against glabellar width (variate K_1) growth seems to proceed isometrically in these two variates. The smallest specimen measured has a glabellar length of 2.4 mm and the largest of 14.0 mm.

Holaspid period: All of the complete individuals that were measured, which includes four specimens with a glabellar length of 2.5 mm or less, have a full complement of thirteen thoracic segments and are therefore holaspides.

Blindness: Three specimens which have a glabellar length below 2.5 mm were apparently blind. In these specimens the eye socle on the fixed cheek is particularly broad and its dorsal surface comes into contact with the outer margin of the palpebral lobe, thus leaving no void which could accommodate the visual surface (lenses) of the eye. One specimen with a glabellar length of 2.5 mm exhibits a small opening between the eye socle and palpebral lobe. All cephala with a glabellar length greater than 2.7 mm show a gap between the palpebral lobe and the eye socle. Calymene tuberculosa seems to have been capable of (dorsal) sight sometime after its glabella was more than 2.5 mm in length. As with other calymenid species, the eye lenses have not been observed; the circumocular suture must have been particularly efficient in releasing the visual surface of the eye.

Contact of lobe 2p and genal buttress: Schrank (1970) demonstrated that in juvenile cranidia of certain species of Calymene the second lateral lobe is not in contact with the fixed cheek and that they only meet later in ontogeny. The four measured specimens with a glabellar length of below 2.5 mm all lack this contact, though they do show an incipient genal buttress. The smallest specimen observed with 2p lobe and buttress in contact has a glabella 2.8 mm long. The largest specimen recorded without this contact has a glabella 3.0 mm long. In between 2.8 mm and 3.0 mm there are several specimens which only just have the second lobe touching the genal buttress. It seems that it was during this period of growth that this structure was formed in C. tuberculosa.

In summary, the smallest recorded specimen (glabella 2.4 mm long) is an holaspis which was also blind and has no contact between lobe 2p and the incipient genal buttress. After the glabella had reached a length of about 2.5 mm, vision was attained. Between about 2.8 mm and 3.0 mm the second glabellar lobe meets the genal buttress.

Ornamentation: The tubercles on the smaller holaspides are relatively larger.

Genal spines: Considering that many of the cranidia are rather small it is perhaps surprising not to have observed any genal spines, but most of these specimens are isolated individuals which have been somewhat abraded, and this may account for their absence. Some of the small cranidia do show the posterior margin to swing slightly backwards near the genal angle.

DISCUSSION. Dalman did not figure this species when he erected it in 1827 but from his description (especially of the axial rings) there is no doubt as to its identity. Some of Dalman's material from his "Om Palaederna" paper is now lost. I am informed (Dr. V. Jaanusson, pers. comm.) that the original specimen(s) of C. tuberculosa, which should be housed in the Paleontological Institute of Uppsala University, is amongst those missing, and I have designated a neotype for Dalman's taxon. Schrank (1970) claims C. breviceps Raymond, 1916 to be synonymous with C. tuberculosa Dalman, 1827, but I consider them to be separate species. The distinguishing features of tuberculosa are given in the diagnosis and its relationship to breviceps is discussed below.

C. tuberculosa is probably the most common calymenid from Gotland. McLearn (1924) has recorded it from the Ross Brook Formation and questionably from the Beechhill Formation of Arisaig. Both these groups of strata are of Llandovery age (Berry & Boucot 1970). Although McLearn describes the extremities of the thoracic axial rings in the Arisaig specimens as having prominent tubercles, it is not clear from the figures if they are of the same type as in tuberculosa, and his material would benefit from re-illustration. McLearn's description of the anterior border and preglabellar furrow could apply to the Swedish taxon, but a time span from the Beechhill Formation (lower Llandovery) to the Mulde Beds (upper Wenlock) is suspiciously long for one species of Calymene.

Schrank (1970) has described some specimens of tuberculosa from glacial erratics of upper Wenlock age, and some from the Mulde Beds of Gotland. Extra information on the Gotland material is presented herein, especially with regard to the ventral morphology of the cranidium, hypostome and rostral plate. The hypostome is similar to many other species of Calymene in having a protuberance on the anterior lobe, but in tuberculosa it is subconical rather than 'hooked' or spine-like, and it is positioned very far down the anterior lobe - near to the conspicuous maculae.

Specimens (SM A84000-007) collected by Dr. R.B. Rickards from the very base of the Wenlock Limestone of Wenlock Edge have proved to be the first examples of tuberculosa recorded from the British Silurian. They are slightly younger in age than the Gotland material from the Mulde Beds (see Cocks et al. figs. 2 and 9).

C. minimarginata Schrank, 1970, which was erected on specimens obtained from glacial boulders of Ludlovian age, is similar to tuberculosa in having a fairly short anterior border. It differs from tuberculosa mainly through its less convex glabella (sag.), wider preglabellar furrow, and less strongly sloping (tr.) fixed cheeks (Schrank 1970, p.131).

OCCURRENCE. Mulde Beds (upper Wenlock) of Gotland - especially from Djupvik in the parish of Eksta. Two feet above the base of the Wenlock Limestone, tabular limestone lithofacies of the non-reef area, road section between Longville in the Dale and Stanway, Wenlock Edge (Nat. Grid. Ref. SO 5399 9275). N German glacial erratics of upper Wenlock age. Questionably from the Llandovery of the Arisaig area. Kaljo (1970, p. 154) records a Calymene cf. tuberculosa from the Jaani Stage (= lower and middle Wenlock) of Estonia.

Calymene breviceps Raymond, 1916

Plate 18, figs. 3-8; Plate 19, figs. 1-7.

1916 Calymene breviceps, sp. nov.; Raymond, p. 27, pl. 3, fig. 11.

1919 Calymene breviceps Raymond; Foerste, p. 78, pl. 18, fig. 7.

1967 Calymene breviceps Weller; Campbell, pp. 27, 28.

1970 Calymene breviceps Raymond; Schrank, pp. 116, 132.

1971 Calymene breviceps Raymond; Whittington, p. 460, pl. 83, figs. 1-5.

HOLOTYPE. A damaged, complete specimen; MCZ 640; figured Raymond 1916, pl. 3, fig. 11 and Whittington 1970, pl. 83, figs. 1-5.

TYPE STRATUM AND TYPE LOCALITY. Waldron Shale (= upper Wenlock in age), Waldron, Indiana, U.S.A.

MATERIAL. Twenty four specimens, DJS/100-124. Presented Mr. D. Mikulic.

DIAGNOSIS. Species of Calymene with exceedingly short (sag. & exs.) anterior border and relatively long, convex (sag.) glabella. Glabella (in dorsal view) often reaches in front of and obscures the underlying anterior border. In frontal view rostral suture gently arched, outer side of anterior border widens slightly toward facial suture.

DISCUSSION. The holotype of this American species has recently been described, figured and discussed (Whittington 1971). The cranidium of C. breviceps is of similar gross morphology to that of C. tuberculosa, both species are upper Wenlock in age, and Schrank (1970) regarded breviceps as a junior synonym of tuberculosa. Whittington (1971) noted several differences between the holotype of Raymond's taxon and the specimens of tuberculosa figured by Schrank, and he preferred to regard them as distinct species pending evidence from more material of breviceps. Mr. D. Mikulic has kindly sent me some specimens from the Waldron Shale of Waldron, Indiana, which allow breviceps to be more adequately defined and at the same time resolve the question of its relationship to tuberculosa.

Whittington considered the holotype of breviceps to have a relatively longer glabella, relatively smaller lobe 2p (compared to lobe 1p) and a shorter anterior border than in the Swedish species. From the cranidia I have examined the anterior border of breviceps is constantly and distinctly shorter than in tuberculosa. This difference alone is considered sufficient to maintain them as separate species. In dorsal view the anterior border of tuberculosa is clearly visible in front of the glabella as a narrow rim. The border of breviceps is visible only between the facial suture and the abaxial margin of the glabella; this is not only because the anterior border is exceedingly short, but also because the frontal glabellar lobe is more swollen than in tuberculosa and overhangs the border. Moreover, as seen in frontal view the outer side of the anterior border of breviceps is weakly arcuate and widens slightly from the median line to facial suture; in tuberculosa it is strongly arcuate and of a uniform width (sag. & exs.).

Lateral lobe 2p is slightly smaller in some specimens of breviceps but this distinction is not constant in all the cranidia examined. The frontal lobe projects farther in front of the fixed cheeks in the American than the Swedish species. Both taxa show node-like swellings on the lateral parts of the axial rings, but the evidence as yet suggests that in breviceps they are not so conspicuously pointed as in tuberculosa (see Whittington 1971, p. 461 and here, DJS/102). The rostral suture of tuberculosa is more strongly arched though both species show quite a marked vaulting of the inner arc of the border sector.

Whittington (1971) described the pygidium of breviceps as lacking interpleural furrows (though they appear to be very faintly suggested on some of his illustrations). The pygidia I have of breviceps are not well preserved, but this may be a further difference between the two species. The external ornamentation appears to be generally similar in breviceps and tuberculosa.

The specimen referred to by Whittington (1971, p. 461) as Calymene cf. breviceps from the Brownsport Formation (= late Wenlock) of Tennessee, and suspected by that author to be a separate species, must now be regarded as such. In addition to the distinctions given by Whittington, C. cf. breviceps has a prominent intermediate lobe in the fork of lateral furrow 1p and seems to have a deeper occipital furrow than in breviceps. The arching and width of the outer side of the anterior border (frontal view) in C. cf. breviceps is like that of C. breviceps (see Whittington 1971, pl. 83, fig. 8), but the length of the dorsal side of the anterior border is more like that of C. tuberculosa. The nature of the anterior border in C. cf. breviceps seems to be intermediate between the other two species.

The cranidium described by Lane (1972, p. 359, pl. 64, figs. 6, 7) as Calymene sp. from strata of probable upper Wenlock age from Greenland also belongs in the tuberculosa - breviceps group. Lane differentiated it from breviceps on account of its coarser ornamentation, subparallel glabellar sides and more highly convex (sag.) glabella. It also has at least four glabellar lobes (Lane, p. 359, pl. 64, fig. 7a) a very rounded outline to the frontal glabellar lobe and an embayment in the abaxial wall of the axial furrow in front of the genal buttress - thus further distinguishing it from breviceps. Nevertheless the very short anterior border, very strongly projecting frontal lobe and highly convex glabella of the Greenland cranidium make a relationship closer to breviceps than to tuberculosa probable (see Lane, pl. 64, figs. 6a, 7a).

OCCURRENCE. Waldron Shale of Indiana, U.S.A.

Calymene interjecta Hawle & Corda, 1847

Plate 19, figs. 8, 9; Plate 20, figs. 1-9; Plate 21, figs. 1-11.

1847 Calymene interjecta; Hawle & Corda, p. 86.

1852 Calym. interjecta Cord.; Barrande, p. 570, pl. 19, figs. 20, 21, ? pl. 43, figs. 44, 45.

1968 Calymene (Calymene) interjecta interjecta Hawle et Corda, 1847; Pillet, p. 12, pl. D, figs. 5, 7, 8, ? pl. F. fig. 3, non planche-texte 1, figs. 7, 8.

? 1968 Calymene interjecta H. & C.; Pribyl & Vanek, pp. 426, 427. (listed only; specimens not examined).

1969 Gravicalymene interjecta Hawle & Corda 1847; Alberti, pp. 413, 414.

1970 Calymene interjecta; Marek in Horny & Bastl, p. 179.

1971 Calymene interjecta; Whittington 1971, p. 363.

1972 Calymene hornyi Vanek; Chlupac (pars), p. 168.

LECTOTYPE. Designated Marek in Horny & Bastl 1970, p. 309; internal mould of an incomplete cranidium, NMP It340, CF 1217; figured Barrande 1852, pl. 19, fig. 21, and here Pl. 21, figs. 9-11.

TYPE STRATUM AND TYPE LOCALITY. Lodenice Limestone, Pragium (lower Devonian), Luzce, Bohemia.

PARALECTOTYPES. Internal mould of incomplete enrolled specimen, NMP It339, CF 1218, figured Barrande 1852, pl. 19, fig. 20, and here Pl. 21, fig. 7 ; internal mould of pygidium, NMP It876, figured Barrande 1852, pl. 43, figs. 44, 45.

ADDITIONAL MATERIAL. More than thirty specimens (cranidia, pygidia and free cheeks): NMW 72.29G.165-172; I Ch 3943, I Ch 3946-947, I Ch 3949, I Ch 39951-955, I Ch 3957; UUG p5762 (5 specimens), UUG 5764 (6 specimens).

DIAGNOSIS. Species of Calymene with short (sag.) anterior border - dorsal side of which is flat, turns sharply over at anterior margin, outer side descends slightly forward to rostral suture. In frontal view rostral suture extremely broadly arched. Glabella subrectangular to weakly bell-shaped. Inflated frontal lobe projects in front of fixed cheek. Lobe 4p present. Palpebral lobe centred opposite furrow 2p.

DESCRIPTION. Glabella is subrectangular to weakly bell-shaped in outline, about 1.2 times as long as wide, protrudes in front of fixed cheek. Occipital ring about as wide as glabella, gently convex in profile, narrows behind lobe 1p to axial furrow where it is about one third its sagittal length. Occipital furrow quite sharply incised, deepest abaxially. Large, subquadrate lateral lobe 1p is slightly less than one third as wide as glabella and quite strongly swollen, separated from median lobe by shallow furrow. Furrow 1p very deep abaxially, runs inwards and gently backwards between first two lateral lobes, bifurcates at median lobe and has small intermediate lobe within this fork. Papillate lobe 2p is transversely elongate, confined adaxially by shallow furrow, joined with somewhat pointed genal buttress. Furrow 2p transversely directed. Lobe 3p bounded by distinctly impressed furrow 3p. Very small lobe 4p present low down on glabellar side. Frontal lobe well inflated, has gently convex anterior margin (in dorsal view), slightly undercut frontally and laterally by preglabellar furrow. Median lobe of glabella broadens considerably from occipital furrow towards frontal lobe. In lateral profile surface of glabella stands well above fixed cheek, is mildly convex and slopes gently downwards between occipital furrow and furrow 2p, descends very steeply on anterior face of frontal lobe.

Axial furrow narrow around lobe 1p, only slightly wider between furrow 2p and preglabellar furrow, on some specimens a broad (exs.) inflation (? eye ridge) runs down abaxial wall opposite furrow 3p, most anterior part of abaxial wall trends inwards a little. Anterior pit sited in axial furrow below posterior part of frontal lobe. Preglabellar furrow very narrow (sag. & exs.) and extremely shallow, its anterior side is horizontal or slopes fractionally upwards to pass smoothly into anterior border. Dorsal side of anterior border is only about one tenth to one thirteenth as long (sag.) as glabella, it turns sharply through ninety degrees at anterior margin, outer side of border falls slightly forwards to rostral suture. Anterior margin weakly to moderately convex forwards. In frontal view rostral suture extremely broadly arched.

Posterior border furrow moderately wide (exs.), posterior side more steeply sloping than anterior side. Postocular part of fixed cheek is inclined gently downwards from palpebral lobe to posterior border furrow (see lateral view), abaxially from palpebral lobe it bends down very steeply towards genal angle (see frontal view). Preocular part of fixed cheek is inclined very steeply forwards and downwards, inner anterior corner turns somewhat inwards. Middle of palpebral lobe is opposite (tr.) anterior margin of 2p lobe or 2p furrow. In frontal view fixed cheek between palpebral lobe and genal buttress is moderately convex. Posterior branch of facial suture runs transversely for a short distance, then turns sharply backwards to cross lateral border furrow where it swings more backwards before bending slightly outwards to meet posterior margin. Anterior branch runs forwards and inwards.

Free cheek bears small eye socle. Lateral border furrow quite narrow and U-shaped. Broad lateral border rolls over and under more steeply anteriorly than posteriorly.

Hypostome and rostral plate unknown.

Pygidial axis has seven rings, in lateral profile is gently arched. Five or six ring furrows are complete and deepest abaxially; seventh ring furrow only marked medially on sharply rounded terminal axial piece. Axial furrow weakest posteriorly. Pleural region slopes steeply outwards from axial furrow, becomes vertical abaxially, curls under slightly at lateral margin. Five pleural furrows are sharply impressed and relatively short. Interpleural furrows are far less distinct and much longer than pleural furrows but do not reach lateral margin, they are very weakly developed on inner part of pleural region, best marked at axial furrow and distally. Postaxial sector falls steeply from axis, limited either side median line by two ridges (? anterior pleural bands of sixth pleurae) which run backwards and downwards from junction of sixth ring furrow and axial furrow.

Glabella, anterior border, fixed cheek and inner part of free cheek have medium to large - sized rounded tubercles. Small tubercles present in posterior border furrow and lateral border furrow. Dorsal part of lateral border has rounded medium-sized tubercles, on the lower part tubercles are more ovate. Pygidial axis and outer part of pleural region have small, closely spaced tubercles and granules. On inner part of pleural region tubercles are much more scarce.

Some specimens show a small spine like projection on outer part of lobe 3p.

DISCUSSION. This taxon has been systematically treated by only one author (Pillet 1968) since Barrande (1852) enlarged upon Hawle & Corda's (1847) brief description. The specimens figured by Barrande were originals of Hawle and Corda (see Marek *in* Horny & Bastl 1970), and one of these has subsequently been selected as the lectotype. *C. interjecta* represents one of the few species of the family to survive into the Devonian, and possibly the last calymenid in the Bohemian succession.

Hawle and Corda's original material is incomplete and in the form of internal moulds; extra topotype specimens would be most useful but the species can still be identified and fairly adequately defined on the basis of the lectotype and paralectotype cranidia. The three cranidia figured by Pillet (1968) from the type stratum help confirm that the diagnostic characters shown by the types are constant for the species. The Lodenice Limestone is Pragium (lower Devonian) in age; additional material assigned here to interjecta is from the Pridoli Formation (= upper Silurian) and I have not seen any specimens referable to this species from the intervening Lochovium (= lowest Devonian). The disparity in time between the Pridoli and Pragium is not inconsiderable, but the Pridoli cranidia show no significant differences from the younger type material and I have considered them to be conspecific. The type cranidium has a very slightly convex anterior border opposite (exs.) the axial furrow and a more distinct intermediate lobe than the Pridoli cranidia, but this can be accounted for by its much larger size.

Some variation is apparent: Most specimens have a weakly arched anterior margin (dorsal view) though in others it is almost straight or it can be moderately convex; the outline of the frontal glabellar lobe is gently convex forwards but it can be somewhat more blunt; and the small spine-like projection on lobe 3p (as in NMW 72.29G.176) is not present on all cranidia.

Pillet (1961, 1968) has erected three subspecies of C. interjecta, two of which come from the uppermost Silurian of N Africa and the other from the lower Devonian (Pragium) of Bohemia. C. interjecta africana Pillet, 1961, C. interjecta hollardi Pillet, 1968 and C. interjecta vaneki Pillet, 1968 all show an uninterrupted course to the axial furrow, no papillate lobe 2p and no trace of an opposing genal buttress. As a consequence they should be removed from Calymene. Alberti (1969) has previously attributed interjecta africana and the nominate subspecies to Gravicalymene, but the latter assignment is clearly mistaken.

The following species have been described (Pillet 1968) from the upper Silurian and lower Devonian of Europe and N. Africa: C. reperta Oehlert, 1889; C. oehlerti sp. nov.; C. erbeni sp. nov.; C. caillaudi sp. nov.; C. ? curvicauda R. & E. Richter, 1943; C. bureaui sp. nov. and C. peneaui sp. nov. The last two species were referred to a new subgenus, Paracalymene. The stratigraphical and geographical occurrence of all these species suggests that they may be related to C. interjecta, yet only C. erbeni seems possibly to belong in Calymene. C. ? erbeni is from the lower Devonian (Emsian) of Germany; in the form of its glabella, fixed cheek and preglabellar area it can be allied with C. interjecta, though a more detailed comparison is precluded because of the poor preservation of the German taxon.

On the basis of its short, flat anterior border, C. interjecta can be placed in Schrank's (1970)species group four which includes C. tuberculosa, C. breviceps, C. minimarginata and C. hadyardensis.

However, it is more of an open question in this instance whether the anterior border can be used as an indicator of relationship, as interjecta is widely separated, both in space and time, from the other species. Of these, C. breviceps is quite different from interjecta and the detailed morphology of hadyardensis is unknown. A steeply sloping frontal lobe and a glabella which protrudes well above the fixed cheek are common to both tuberculosa and interjecta, and minimarginata is similar to the Bohemian species in its fairly straight anterior margin (dorsal view) and gently arcuate rostral suture. C. tuberculosa differs from interjecta by, amongst other things, its lack of a 4p lobe, much more strongly arched rostral suture, more posteriorly positioned eye, no intermediate lobe, sharply pointed nodes on the occipital ring, and a totally different pygidium. C. minimarginata has a less inflated frontal glabellar lobe which does not project in front of the fixed cheek or overhang the preglabellar furrow, no 4p lobe, a less strongly sloping (tr.) postocular part to the fixed cheek and a different type of ornamentation.

Whittington (1971, p. 463) referred to the illustrations of Pillet (1968) and suggested that C. interjecta exhibits the "beginning of the development of buttress 3p" which is diagnostic of Papillicalymene from the Ludlovian of Gotland. The broad inflation on the outer side of the axial furrow is interpreted here as the remnant of an eye ridge. There seems nothing in the morphology of interjecta to strongly associate it with the aberrant Swedish genus.

OCCURRENCE. Middle and upper Pridoli (upper Silurian) and Pragium (lower Devonian) of Czechoslovakia. In addition to the Lodenice Limestone interjecta has been recorded (Pribyl & Vanek, 1968) from the Slivenec and Vinarice Limestones which are also Pragium in age; this material has not been described. Specimens of C. interjecta have been referred to Calymene hornyi in biostratigraphical papers on the Bohemian upper Silurian (eg. Chlupac (pars) 1972). C. hornyi is in any case a nomen nudum.

Barrande (1852, p.570) recorded interjecta from the areas around Tetin, Dvorce, Luzce and Lodenice. It should be noted that the paralectotype pygidium (NMP It876) from the Dvorce - Prokop Limestone (= Pragium) at Dvorce shows a wider, more strongly tapering axis than the stratigraphically earlier Pridoli material here assigned to interjecta, as does that pygidium figured by Pillet (1968, pl. F, fig. 3) from the Lodenice Limestone.

Calymene planicurvata Shirley, 1936

Plate 22, figs. 1-7.

1865 Calymene Blumenbachii, BRONGN, var. a, auctorum; Salter, pl. 9, figs. 1a, b. non figs. 2a, b.

1936 Calymene planicurvata sp. nov.; Shirley, p.412, pl. 30, figs. 6, 7.

? 1938 Calymene planicurvata Shirley; Whittard p. 88.

1970 Calymene planicurvata SHIRLEY, 1936; Schrank, p. 116.

HOLOTYPE. Incomplete internal mould of a cranidium; GSM 19624; figured Shirley 1936, pl.30, figs. 6, 7 and here Pl. 22, figs. 2, 5.

TYPE STRATUM AND TYPE LOCALITY. Bog Quartzite, Idwian Stage (Ziegler et al. 1968, pp. 743-44), Llandovery Series, Bog Mine, Shelve Inlier, Shropshire.

ADDITIONAL MATERIAL. About a dozen isolated cranidia and pygidia.

DIAGNOSIS. Glabella is weakly bell-shaped to subtriangular in outline. No intermediate lobe at inner end of furrow 1p. Frontal lobe quite well rounded, slightly more than 0.6 times as wide as glabella at lobe 1p. Preglabellar area about a quarter as long as glabella. Preglabellar furrow wide and moderately shallow. Anterior border gently to moderately upturned.

DESCRIPTION. Cephalon more than twice as wide as long. Glabella 1.0 - 1.1 times as wide as long, weakly bell-shaped to subtriangular in outline. Occipital ring widest medially, flexes forwards abaxially. Occipital furrow deepest behind the large, subquadrate 1p lobe which is slightly less than one third as wide as glabella. Lateral furrow 1p curves inward and backward; there is no intermediate lobe on the side of central area of glabella. Lobe 2p is subcircular or slightly elongate (tr.), bounded adaxially by shallow furrow. Lobe 3p distinctly swollen, perched on dorsolateral glabellar surface. Some specimens show faint indication of 4p lobe. Frontal lobe slightly more than 0.6 times as wide as glabella at lobe 1p; anterior margin of frontal lobe well rounded in outline, projects just in front of fixed cheek, falls steeply to preglabellar furrow; sides of frontal lobe trend forward and inward.

Axial furrow rather deep around lobe 1p and in front of genal buttress, its outer wall is steeply inclined between furrow 2p and deep anterior pit which is sited on inner side of axial furrow below posterior part of frontal lobe. Preglabellar area is about a quarter as long as glabella. Preglabellar furrow rather wide (sag. & exs.) and shallow, passes smoothly forwards into anterior border which is gently to moderately upturned. In dorsal view anterior margin is broadly arcuate.

Posterior border furrow is widest (exs.) mid-way between axial furrow and facial suture. Posterior branch of facial suture runs outwards then turns sharply backward to lateral border where it bends more backward and finally slightly outward to posterior margin. Anterior branch of suture runs forwards and fractionally inwards. Palpebral lobe centred opposite furrow 2p.

Hypostome, rostral plate and thorax unknown. Axis of pygidium is quite strongly convex,has at least six axial rings. Anterior three rings are very slightly inflated near axial furrow. Ring furrows are deepest abaxially. Axial furrow shallowest behind sharply rounded terminal axial piece. Pleural furrows are well marked; interpleurals deepest distally, absent on inner part of pleural region.

Ornamentation unknown.

DISCUSSION. The above description is based on quite well preserved, but internal mould specimens (Holotype, SM A59964, DJS/147, DJS/148).

Extra material of this species has been collected from Round Hill near Bog Mine, but as yet no external mould is at hand to facilitate a detailed comparison with specimens of the other Silurian taxa described herein, most of which have the cuticle extant. C. planicurvata is probably closely related to C. mimaspera Schrank, 1970 and C. aff. mimaspera (of the present paper), and to a lesser extent C. aspera Shirley, 1936.

C. mimaspera can be distinguished by its shorter preglabellar area (about one sixth as long as the glabella), shorter preglabellar furrow, convex (sag.) anterior border, and wider fixed cheek in front of the palpebral lobe. All these differences except the last also separate C. aff. mimaspera from planicurvata, though aff. mimaspera is above all identified by its wider frontal lobe which results in the glabella taking on a subrectangular appearance. The glabellar outline and narrow frontal lobe of planicurvata are very similar to those of the later C. aspera, but amongst other things a conspicuous intermediate lobe at the inner end of furrow 1p and a much shorter preglabellar area serve to differentiate the Wenlockian species.

A less upturned anterior border and a shallower preglabellar furrow are the principal differences of C. planicurvata from the Llandovery taxa C. frontosa, C. carlops and C. subdiademata.

OCCURRENCE. Apart from the type horizon and locality, Shirley (1936, p. 412) recorded planicurvata from Hope Quarry, near Minsterly. Shropshire. A graptolite find from strata near the base of Hope Quarry indicates an Idwian age. (Ziegler et al. 1968, p. 744). Whittard (1938) listed the species from the Pentamerus Beds and Purple Shale (Idwian to Telychian) of Shropshire.

Calymene cf. C. mimaspera Schrank, 1970

Plate 23, figs. 2, 3, 7-9.

MATERIAL. RSM 1911.62.1689; BM It9147, BM 44297; BU 38, BU 247, BU 554, BU 664 (all Hollcroft Colln.), BU 357 (Ketley Colln.).

OCCURRENCE. Wenlock Limestone, Dudley.

DISCUSSION. C. mimaspera was established on the basis of material from Graptolithengestein glacial erratics of Wenlock to lower Ludlow age from N Germany. It was discriminated from C. aspera Shirley, 1936 by its much more weakly arched anterior margin, wider fixed cheek, the absence of an intermediate lobe at the inner end of furrow 1p, and a less strongly inclined free cheek. A comparison of Schrank's (1970, pl. 2, figs. 4-6, pl. 3, figs. 3, 5-7) illustrations with those of aspera given here suggests that mimaspera also has a less subtriangular cephalic outline, a less anteriorly projecting frontal lobe, a somewhat more stout and convex (sag.) anterior border, less steeply descending (tr.) fixed cheek and finer glabellar tubercles.

In the Wenlock Limestone of Dudley there is a species which more closely resembles C. aspera than C. blumenbachii yet differs from Shirley's taxon in certain characters. These characters are the same as some of those that distinguish mimaspera from aspera - the nature of the anterior margin, fixed cheek, glabellar outline, anterior border, the absence of an intermediate lobe - and as far as can be determined the unnamed Dudley species is nearer to mimaspera than to any other Calymene. It appears to differ from mimaspera in lacking an inflated node on the occipital ring, having a slightly more projecting frontal glabellar lobe and a narrower posterior border furrow (compare Schrank 1970, pl. 2, fig. 4). A comparison of the glabellar ornament of mimaspera with that of the Dudley specimens is unfortunately precluded by the surface abrasion of the latter. The differences outlined are not great but I hesitate to assign the Dudley material with certainty to mimaspera until the type material has been examined.

The specimens of C. cf. mimaspera are preserved in a muddy limestone or shale, not the typical highly crystalline Dudley Limetone that characteristically yields C. blumenbachii. Shaly intercalations are present throughout much of the Wenlock limestone of the Dudley area (Wrens Nest and Dudley Castle Hill) and there may have been some facies control on this species. It is also worth noting that small patches of Wenlock Shale and lower Ludlow Shale are known to outcrop in this district (Butler 1939), and it is possible that some of the old museum specimens labelled 'Wenlock Limestone' are in fact from these other two horizons.

Calymene sp. 1

Plate 22, figs. 8, 9.

MATERIAL. A damaged, complete specimen; BU 183 (Hollcroft Colln.).

OCCURRENCE. Wenlock Limestone, Dudley.

DISCUSSION. A Wenlockian species of Calymene was prepared from the ventral side in order to show its internal morphology. The identity of the species is unknown as removal of the sediment encasing the dorsal side of the specimen would result in fragmentation of the exoskeleton, and the anterior border has been destroyed. The specimen is embedded in a matrix identical to that in which C. cf. mimaspera occurs (see discussion of that species). The hypostome is similar to that of C. blumenbachii but does not have such a prominent median spine on the anterior lobe; in this respect it can be more closely compared with C. tuberculosa Dalman.

The construction of the articulation processes of the thoracic pleurae, the form of the pleural doublure, stops for enrollment, and apodemes are all identical to those described by Campbell (1967, p.26) in C. clavicula from strata of upper Wenlock/lower Ludlow age in Oklahoma.

Calymene aff. C. mimaspera Schrank, 1970

Plate 23, figs. 1, 4-6.

MATERIAL. One cranidium, DJS/144, collected David J. Siveter and P. Turner, 1971.

OCCURRENCE. Buildwas Beds (= lower Wenlock), cutting on the eastern bank of Harley Brook, approximately 200 yards S of junction between Harley Brook and Merrishaw Brook, near Domas, Welsh Borderlands.

DESCRIPTION. Cranidium 2.1 times as wide as long. Glabella 1.2 times as long as wide, subrectangular in outline. Occipital ring only one fifth as long (sag.) as wide, gently convex in profile, inflated into small node at axial furrow where it is flexed forwards. Lobe 1p less than one third as wide as glabella; furrow 1p is deep, slightly narrower than axial furrow outside lobe 1p, curves inwards and progressively more backwards, gives off very short anterior branch around lobe 2p; no intermediate lobe on side of median glabellar lobe. Lobe 2p papillate, separated from median lobe by shallow furrow. Lobe 3p subelliptical in dorsal view, runs down side of glabella; furrow 3p very distinct. Frontal lobe three-quarters as wide as glabella at lobe 1p, anterolateral and anterior margins well rounded in dorsal view, most anterior tip projects in front of fixed cheek.

Axial furrow moderately deep at occipital ring and posterior margin of lobe 1p, is fairly wide and becomes progressively deeper around lobe 1p, runs under bridge of genal buttress and lobe 2p, from furrow 2p to preglabellar furrow it is a deep, constantly wide trench. Anterior pit in base of furrow half way along the side of frontal lobe. Preglabellar furrow about as wide medially as axial furrow in front of lobe 2p, widens slightly abaxially, is moderately deep, anterior side slopes forwards and upwards at about forty degrees. Anterior border about half as long (sag.) as lobe 1p, slightly swollen opposite axial furrow, in lateral profile dorsal and outer sides are quite strongly convex. Anterior margin and rostral suture broadly arched.

Fixed cheek is as wide as neck ring. Posterior border furrow lens-like, widest (exs.) at mid-length. Posterior branch of facial suture runs outwards then backwards to lateral border, then more backwards and finally very slightly outwards to posterior margin. Anterior branch curves forwards and very gently inwards. Palpebral lobe centred opposite anterior part of lobe 2p, about as long as lobe 2p, outer margin slightly pointed. In transverse section, preocular part of fixed cheek and outer vertical wall of axial furrow form a right-angle. Furrow between fixed cheek and anterior border runs outward and fractionally forward.

Glabella, inner part of fixed cheek, and anterior border covered with rather closely spaced fine tubercles and granules. On outer part of fixed cheek and occipital ring tubercles much more scarce. Deepest part of all furrows smooth.

DISCUSSION. This relatively large, well preserved cranidium closely matches _C_. _mimaspera_ and unlike _C_. cf. _mimaspera_ also displays an inflated node on the occipital ring as in the N German species. Points of distinction from _mimaspera_ include a relatively wider frontal lobe - which gives the glabella a subrectangular appearance, a narrower (tr.) preoccular part to the fixed cheek, a trench-like axial furrow in front of lobe 2p with a vertically inclined outer wall, and much finer ornamentation on the fixed cheek near the genal buttress. Until a knowledge is gained of the variation in the Welsh Borderland species, the significance of these distinctions remains unknown; they would provide a basis for diagnosing a separate species of the mimaspera type if proved to be constant throughout the Buildwas Beds population.

The anterior broders of C. mimaspera, C. aff. mimaspera, and C. cf. mimaspera are not far removed from that of C. neotuberculata Schrank, 1970, but the latter species can be immediately distinguished by its very much narrower cranidial axial furrow, especially around lobe 1p.

Calymene aspera Shirley, 1936

Plate 24, figs. 1-7; Plate 25, figs. 1-6.

1936 Calymene aspera sp. nov.; Shirley, p. 412, pl. 30, figs. 8-10, pl. 31, fig. 5.

1954 Calymene (C.) aspera Shirley 1936; R. & E. Richter, p. 19.

1968 Calymene aspera Shirley; Haas, p. 99.

1970 Calymene aspera Shirley, 1936; Tomczykowa, pp. 71, 75, non fig. 5b.

1970 Calymene aspera SHIRLEY, 1936; Schrank, pp. 115, 123, 125.

HOLOTYPE. Damaged complete specimen; BM It28659; figured Shirley 1936, pl. 30, figs. 8-10, pl. 31, fig. 5, and here Pl. 24, figs.1-3, 6.

TYPE STRATUM AND TYPE LOCALITY. Wenlock Limestone (top Wenlock Series, M. ludensis zone), Dudley.

ADDITIONAL MATERIAL. Five complete specimens, BM In28651-653, BM In28655, BM In28659.

DIAGNOSIS. Cephalon subtriangular in outline. Glabella subtriangular to weakly bell-shaped; well rounded frontal lobe is about two-thirds the width of glabella at lobe 1p; very distinct intermediate lobe. Anterior border inclined gently to moderately upwards. Preglabellar area is about one seventh as long as glabella. Anterior margin (dorsal view) and rostral suture (ventral view) are quite strongly arched. Postocular part of fixed cheek 0.7 - 0.75 as wide as occipital ring, strongly bent downwards (tr.).

DESCRIPTION. Cephalon subtriangular in outline, about 1.8 to 2.0 times as wide as long. Glabella is subtriangular to bell-shaped, about 1.1 times as long as wide, its sides are quite strongly convergent anteriorly, projects well in front of and stands prominently above the fixed cheeks. Occipital ring slightly narrower than width of glabella, at median line is slightly longer than lobe 2p, narrows abaxially and is flexed forwards at axial furrow where it is slightly inflated. Occipital furrow moderately deep and widest medially, very much deeper and narrower distally. Lobe 1p subrectangular. Lateral furrow 1p is deepest and widest at axial furrow, narrowest between lobes 1p and 2p, bifurcates adaxially into very distinct anterior and posterior branches. Posterior branch curves backwards then inwards; anterior branch is more straight and runs forwards and inwards. A conspicuous intermediate lobe is present within fork of 1p furrow. Lobe 2p is subcircular to subovate, more isolated from median lobe than lobe 1p, quite strongly convex (tr. & exs.). Furrow 2p is transversely directed. Lobe 3p distinctly inflated, about as large as intermediate lobe but a little more transversely elongate, confined anteriorly by well marked furrow 3p. Weak lobe 4p present on holotype. Sides of frontal lobe run forward and slightly inwards, anterolateral margins well rounded, anterior margin fairly convex forwards and descends quite steeply to preglabellar furrow. Frontal lobe is weakly undercut by axial and preglabellar furrows and is about two-thirds the width of the glabella at lobe 1p.

Axial furrow moderately wide and deep outside lobe 1p, is slightly wider between furrow 2p and preglabellar furrow. Anterior pit sited below 4p lobe. Preglabellar furrow extremely shallow and rather narrow (sag. & exs.). Preglabellar area fairly short - about one seventh as long as glabella; in lateral profile dorsal side of anterior border projects forwards and very gently to moderately upwards, its outer side descends slightly forwards to rostral suture. In dorsal view anterior margin is strongly arched forwards.

Posterior border furrow fairly shallow, moderately wide (exs.). Postocular part to the fixed cheek is inclined gently downwards from palpebral lobe to posterior border furrow, falls very steeply from axial furrow to genal angle; preocular part descends very steeply forwards, is slightly wider (tr.) than palpebral lobe which projects quite steeply upwards and is centred opposite the middle or anterior part of lobe 2p. Posterior branch of facial suture trends outwards and slightly backwards from eye lobe before turning sharply backwards to run to lateral border on which it turns more backwards to cut genal angle; anterior branch runs forwards and inwards to anterior margin where it turns abruptly inward on outer side of anterior border to connect with rostral suture.

Free cheek descends almost vertically from narrow eye socle; lateral border furrow broadly U-shaped, weakest posteriorly; lateral border curls over and under.

Rostral suture and rostral plate both quite tightly arched.

Thorax has thirteen segments. Axis is very strongly vaulted (tr.), each axial ring is of constant width (sag. & exs.), inflated into weak node at axial furrow where it is flexed slightly forwards. Pleural furrow U-shaped, divides moderately convex (exs.) posterior pleural band from shorter (exs.) anterior pleural band.

In dorsal view pygidium is shaped like an isosceles triangle. Axis is between 0.4 and 0.5 times the total width, has seven axial rings, is strongly arched (tr.). Ring furrows weakest medially, seventh ring furrow fails to reach axial furrow. Pleural region falls first very steeply, then vertically away from axial furrow. There are five well marked pleural furrows which fail to reach lateral margin; interpleurals are slightly longer, most distinct distally, very faint adaxially but are continuous to axial furrow. Terminal axial piece somewhat rounded; posterior margin of postaxial sector rather pointed at median line.

Ornament on inner, anterior part of fixed cheek consists of closely spaced tubercles of many different sizes, the larger ones of which are often perforate. Anterior border, abaxial part of fixed cheek, free cheek, and outer part of pygidial pleural region all lack the larger tubercles shown by the glabella and have tightly set medium and small tubercles. A few tubercles are scattered on thorax on the axial rings and pleurae with noticeable concentration of larger tubercles on weakly inflated axial nodes.

DISCUSSION. _C. aspera_ is sympatric with _C. blumenbachii_ at Dudley though is far less abundant than Brongniart's species. It differs from _blumenbachii_ in its longer, less upturned anterior border, subtriangular cephalic outline,more subtriangular glabella with a relatively narrower frontal lobe (compared with glabellar width across lobe 1p), more steeply descending (exs.) postocular part to the fixed cheek, more strongly arcuate anterior margin (dorsal view) and rostral suture (ventral view), and a more discrete intermediate lobe at the adaxial end of furrow 1p.

The Wenlockian strata at Penylan Quarry, Cardiff and the adjacent new road cutting have yielded numerous internal mould specimens of _Calymene_ which are best regarded as conspecific, and are here referred to C. aspera. There is variation in the inclination of the anterior border, and in some cranidia it is more upturned than in aspera specimens from Dudley; the border of these cranidia therefore trends towards that of C. blumenbachii but in all the other characters given above which distinguish aspera from blumenbachii, the Welsh specimens are to be compared with aspera.

A comparison of C. aspera with C. mimaspera Schrank,1970 is given above under C. cf. mimaspera.

Shirley (1936, p. 413) noted the resemblance of the highly arched anterior margin (ventral view) in C. aspera and C. tuberculosa and suggested that the two species were related. One may add that those specimens of aspera that have a weakly inclined anterior border (e.g. BM In28653) are not dissimilar to tuberculosa in this character, except it is a little longer in the Dudley species. It is unquestionable, however, that the two are specifically distinct - C. tuberculosa has a different outline to the cephalon, anterior margin and glabella, acutely pointed nodes on the axial and occipital rings, a much less convex (tr.) pygidial axis, distally weaker interpleural furrows, and the lack of an intermediate lobe. C. aspera seems to occupy a somewhat intermediate position between the tuberculosa group of species and those centred around blumenbachii.

OCCURRENCE. Apart from the type locality, from the Wenlock Series of Penylan near Cardiff.

Calymene falcata sp. nov.

Plate 26, figs. 1-6; Plate 27, figs. 1-8.

DERIVATION OF THE NAME. From the Latin, falcatus, sickle-shaped, referring to the outline of the axial furrow around lateral glabellar lobe 1p.

HOLOTYPE. Slightly damaged complete specimen; RM Ar31438; Pl. 26, figs. 1-6.

TYPE STRATUM AND TYPE LOCALITY. Mulde Beds (= upper Wenlock), Fröjel, Gotland.

ADDITIONAL MATERIAL. Five complete, but damaged specimens RM Ar27339, RM Ar27379-380, RM Ar47709, SGU Hedström's sample no. 28; one incomplete cranidium, RM Ar27376; one incomplete pygidium RM Ar27377.

DIAGNOSIS. Glabella in front of lobe 2p is subrectangular in outline. Anterior margin of frontal lobe is straight (tr.). Axial furrow sickle-shaped around lobe 1p. Preglabellar area fairly long - about one fifth as long as the glabella. Dorsal surface of anterior border relatively flat in lateral profile, moderately inclined, turns sharply over at anterior margin.

DESCRIPTION. Cephalon about twice as wide as long, anterior margin of cranidium projecting a little beyond general outline. Glabella is bell-shaped, 1.0 - 1.1 times as wide as long. Occipital ring gently convex, of constant width behind central glabellar area, narrows rapidly behind lobe 1p to axial furrow where it is about half as wide as at sagittal line. Occipital furrow V-shaped in section, moderately deep medially, very deep adaxially. Lobe 1p is large and subquadrangular. Furrow 1p widest and deepest abaxially, trends firstly inwards and backwards, more sharply backwards around inner margin of lobe 1p, finally curving inwards at right angles to median line; a small anterior branch runs forwards and inwards. Within adaxial fork of furrow 1p the glabella is broadly inflated. Lobe 2p separated from median lobe by shallow furrow. In front of lobe 2p the glabellar outline narrows sharply and is markedly rectangular. Lobe 3p is rather small compared with lobe 2p. Furrow 3p well marked. Frontal lobe rectangular in outline - abaxial sides exsagittally directed, anterior margin straight (tr.) and projects in front of fixed cheek, antero-lateral corners sharply rounded. In lateral profile dorsal surface of glabella projects well above fixed cheek, it is gently convex upwards and approximately horizontal between occipital furrow and lobe 3p where it begins to descend, finally falling vertically on lower anterior face of frontal lobe.

Axial furrow very shallow and moderately wide at occipital ring; around lobe 1p it is sickle-shaped - widest at a point just posterior to half way along the side of lobe 1p, narrows sharply anteriorly and posteriorly from this point, has a smooth, downward and inward curving outer wall which fractionally undercuts dorsal surface of fixed cheek; axial furrow is deep and widest at furrow 2p, from here to preglabellar furrow it narrows slightly, its outer wall slopes downwards and inwards. Anterior pit situated half-way along the side of frontal lobe. Preglabellar area about one fifth as long as glabella. Preglabellar furrow slightly undercuts frontal lobe. Dorsal side of anterior border is moderately upturned, relatively flat in lateral profile, turns sharply over at anterior margin into a much narrower outer side which descends slightly backwards to rostral suture. Anterior margin fairly well arched in dorsal view.

Postocular part of fixed cheek is about 0.8 - 0.9 times as wide as occipital ring. Posterior border furrow quickly widens (exs.) from axial furrow, fails to reach facial suture. In lateral profile preocular part of fixed cheek falls steeply towards anterior border, postocular part is a little less steeply inclined to border furrow. Fixed cheek between palpebral lobe and genal buttress is gently convex and about horizontal. Palpebral lobe is rather small - about as long or slightly shorter than lobe 2p, centred opposite anterior part of lobe 2p. Posterior branch of facial suture runs outwards then backwards to lateral border, from here more backwards and slightly outwards to genal angle. Anterior branch runs forwards and inwards to anterior margin, then turns sharply inwards to meet rostral suture. Lateral border furrow on free cheek is broadly U-shaped.

Rostral suture fairly strongly arched. Border sector of rostral plate about three times as wide as long. Anterior border of hypostome flexed ventrally; anterior border furrow weakly impressed medially, lacking abaxially. Anterior wings large, anterior pits deep. Lateral border tightly rolled (tr.); posterior border much flatter and expanded into two broad, moderately long spines. Abaxial sides of anterior lobe are steeply inclined away from stout, subcircular, centrally positioned projection; anterior part of anterior lobe is concave (sag.), posterior part gently convex and steeply sloping to weak median furrow. Maculae are ovate, smooth, weakly convex. Posterior lobe is U-shaped.

Thorax composed of thirteen segments. Axis narrows gradually posteriorly. Axial rings fairly convex (sag. & exs.), weakly inflated at axial furrow. Posterior pleural band quite strongly convex in section; pleural furrow deep and U-shaped dorsally, becomes V-shaped and slit-like near flat pleural facet; anterior pleural band is as convex as posterior band.

Axis of pygidium quite strongly convex (tr.), has seven to eight axial rings, at least the first six of which are confined posteriorly by a complete ring furrow. All ring furrows more weakly impressed medially; last ring furrow fails to reach axial furrow. Terminal axial piece bluntly rounded. Inner part of pleural region slopes very steeply away from axial furrow, outer part is vertically inclined. There are five distinctly impressed pleural furrows. Interpleurals are best marked distally, become much fainter adaxially.

Ornament on glabella and inner part of fixed cheek consists of various sized tubercles ranging from large down to small granules. On outer part of fixed cheek, free cheek and dorsal surface of anterior border the larger tubercles are absent. Lateral border, outer side of anterior border and rostral plate have small, closely spaced tubercles of a relatively uniform size. Very fine tubercles in lateral and posterior border furrows and on hypostome. Much of thorax apparently smooth except for a few scattered tubercles; a small concentration of tubercles on axial rings near axial furrow. Small closely spaced tubercles on outer part of pygidial pleural region and medial part of axis.

DISCUSSION. C. falcata is closely related to C. aspera and allied species but the combination of characters given in the diagnosis immediately distinguishes the new taxon from others within this group and from all other members of the genus. Particularly unusual is the crescent or sickle-shaped form of the axial furrow outside lobe 1p, from which the species derives its name. This shape may represent an atavistic trait as it is reminiscent of that shown by earlier species of Pharostoma, though in C. falcata the furrow does not have a flat base and is much deeper than in the distantly related Ordovician genus.

OCCURRENCE. Only known from the Mulde Beds (= upper Wenlock) where it occurs with C. neotuberculata and C. tuberculosa; parishes of Fröjel (type locality) and Eksta (Djupvik).

Calymene blumenbachii Brongniart, 1822

Plate 28, figs. 1-9; Plate 29, figs. 1-8; Plate 30, figs. 1-3.

1822 Calymene blumenbachii; Brongniart, p. 11, pl. 1, figs. 1A-D.

1839 Calymene Blumenbachii Brongniart; Murchison, p. 653, pl. 7, figs. 6, 7, non fig. 5.

1852 Calym. Blumenbachi. Brongn.; Barrande, p. 566, pl. 5, fig. 8 non pl. 19, fig. 10, pl. 43, figs. 46-48.

1852 Calymene Blumenbachi (Brong.); McCoy (pars) in Sedgwick & McCoy, p. 165.

1865 Calymene Blumenbachii, Brongn.; Salter, p. 93, pl. 8, figs. 7, 8, 10, 12-16, non figs. 9, 11, pl. 9, figs. 1, 2.

1868 Calymene ceratophthalma;Woodward, p.489, pl. 21, fig. 1, non fig. 2.

non 1872 Calym. Blumenbachi Brongn.; Barrande, p. 36, pl. 14, fig. 33.

non 1879 Calymene Blumenbachii, Brongniart; Nicholson & Etheridge, p. 140, pl. 10, figs. 2-6.

non 1906 Calymene blumenbachi, Brongniart, 1822; Reed, p. 133, pl. 17, figs. 12, 13.

1933 Calymene blumenbachi BRONGNIART, 1822; Shirley, p. 59, pl. 1, figs. 1-5.

1936 Calymene lata sp. nov.; Shirley, p. 414, pl. 30, figs. 11-13, pl. 31, figs. 1-4.

non 1957 Calymene (Calymene)blumenbachi blumenbachi Brongniart, 1822; Tomczykowa, p. 135, pl. 3, figs. 3, 4.

1959 Calymene blumenbachii Brongniart, 1822; Whittington in Moore, p. O452.

1970 Calymene blumenbachi blumenbachi; Schrank, p. 135, pl. 9, figs. 5, 6.

SYNTYPES. The two specimens mentioned by Shirley (1933, p. 53) which formed the basis for Brongniart's (1822, p.11, pl. 1, figs. 1A-D) description and illustrations, and which were housed in the Geological Laboratories of the Sorbonne, Paris.

The enrolled specimen depicted by Brongniart on pl. 1, figs. 1A, B was regarded by Shirley (1933, p. 53) as "the type". There is no point in formally designating this specimen as the lectotype, as it is possible that the type specimens are now lost. Several attempts have been made by the present author to locate and examine Brongniart's original material, but so far these have met with no success. Fortunately one of Brongniart's specimens has been refigured (Shirley, 1933, pl.1, figs. 1, 2) and the identity of the species is not in doubt.

TYPE STRATUM AND TYPE LOCALITY. Wenlock Limestone (= top Wenlock Series, M. ludensis zone); Dudley.

ADDITIONAL MATERIAL. All of the major British Museums have well preserved material of this species and there is no attempt here to provide a comprehensive list. The total number of specimens must be in excess of 200.

DIAGNOSIS. Species of Calymene with a very short (sag.), low, vertically inclined anterior border the dorsal surface of which is a sharp edge; preglabellar furrow very short, moderately deep; strongly inflated glabella projects well above, and well in front of fixed cheek; distal part of interpleural furrows very distinct; posterior margins of hypostome V-shaped.

DESCRIPTION. Cephalon is subsemicircular in outline, about twice as wide as long. Glabella is weakly to strongly bell-shaped in outline, about 1.0 to 1.1 times as long as wide, projects well in front of fixed cheeks. Occipital ring narrower (tr.) than glabella, very gently convex in profile, in dorsal view is longest medially but shortens gradually abaxially and flexes forwards at axial furrow where it is weakly inflated. Occipital furrow moderately long and not deeply incised behind central glabellar area, becomes slit-like abaxially. Lobe 1p is fairly large, subquadrate, has quite strongly convex outer margin, is strongly swollen, separated from median lobe by very shallow extension of furrow 1p. The latter is deep and widest (exs.) at axial furrow, runs inwards and backwards between lobes 1p and 2p, bifurcates adaxially, longer posterior branch turning first backward then inward, anterior branch directed forward and inward across inner side of lobe 2p. Small intermediate lobe present within fork of furrow 1p. Lobe 2p rather swollen, transversely elongate, papillate. Furrow 2p directed transversely or slightly forwards. Lateral lobe 3p longest (exs.) dorsally, narrows as it runs down side of glabella, confined by distinct though shallow 3p furrow which trends forwards. Small 4p lobe sometimes present. Lateral sides of strongly inflated frontal lobe are inclined vertically and directed exsagittally, anterolateral margins are fairly sharply rounded, anterior outline varies from relatively strongly convex forwards)GSM 19688) to almost straight (BU 413 Hollcroft Colln.). Frontal lobe is about $^7/10$ to $^3/4$ as wide as glabella at lobe 1p. In lateral profile dorsal surface of glabella projects well above fixed cheek, is gently convex between occipital furrow and furrow 2p, falls very steeply at anterior face of frontal lobe which is undercut by preglabellar furrow.

Axial furrow very shallow at occipital ring, narrowest at base of lobe 1p, becomes progressively wider (tr.) and much deeper from here to furrow 1p where it is widest; between genal buttress and preglabellar furrow it is a uniformly narrow, deep trench. Anterior pit is below posterior part of frontal lobe. Preglabellar furrow very short (sag. & exs.), moderately deep. Anterior border is a very short raised rim, in lateral view inner side curves vertically upwards and a little inwards, dorsal surface is quite sharply edged and does not reach far up anterior face of frontal lobe, outer side descends very steeply to rostral suture. Opposite axial furrow anterior border is slightly swollen. Anterior margin gently to moderately convex forwards in dorsal view and upwards in frontal view.

Posterior border becomes considerably wider (exs.) and less convex abaxially from fulcrum. Posterior border furrow widest opposite fulcrum. In lateral profile postocular part of fixed cheek is horizontal or slopes (exs.) very gently to posterior border furrow, preocular part is rather narrow (tr.), slopes steeply downwards and forwards. Furrow between fixed cheek and anterior border is slightly longer (exs.) and somewhat shallower than preglabellar furrow. In frontal view fixed cheek adaxially from palpebral lobe is moderately convex and slopes (tr.) marginally downwards to axial furrow. Palpebral lobe is inclined quite steeply upwards from axial furrow, is longer (exs.) than lobe 2p but not as long as lobe 1p, its outer margin is slightly pointed. Posterior branch of suture runs transversely from palpebral lobe then turns to run onto lateral border where it bends sharply backwards and finally slightly outwards to bisect lateral and posterior margins. Visual surface of eye is reniform. In dorsal view convex free cheek descends very steeply to distinct, U-shaped lateral border furrow. Lateral border turns sharply over and under; doublure reflexed.

Rostral plate composed of border and doublure sectors. Border sector and rostral suture broadly arched; connective suture abaxially convex. Hypostome about 1.2 to 1.3 times as wide as long (through posterior spine). Anterior border very narrow; anterior border furrow weak, only marked medially. Deep pit in large anterior wing. Anterior lobe of median body has a stout, centrally positioned spine. Anterior part of anterior lobe is concave (exs.), posterior part is mildly convex and slopes downwards from spine to very faint median furrow. Oval maculae are very weakly convex and smooth. Crescent-shaped posterior lobe descends posteriorly to two relatively short, flat spines. Posterior margin V-shaped.

Thorax composed of thirteen segments. Axial ring fairly narrow (sag. & exs.), produced into gently inflated node at axial furrow, in lateral profile weakly convex. Articulating half ring fairly wide and shallow medially, deeper and narrower (exs.) abaxially. Posterior pleural band gradually widens to the flat pleural facet around which it forms a narrow bounding rim. Dorsally the pleural furrow is relatively wide (exs.), deep and U-shaped, reduced to a rille-like slit on pleural facet. Anterior pleural band tightly convex (exs.), narrower and slightly lower than posterior band.

Pygidium is slightly less than twice as wide as long. Axis is between 0.4 and 0.5 times the width of pygidium, reaches well above pleural regions, strongly convex (sag.), normally has six or seven axial rings though exceptionally can have eight. First six axial rings defined posteriorly by complete ring furrows which are weakest medially; seventh ring furrow discontinuous - lacking medially and also fails to reach axial furrow. Eighth ring furrow is concave forwards and confined to medial part of rounded terminal axial piece. Axial furrow clearly impressed, weakest posteriorly. Inner part of pleural region falls steeply from axial furrow, outer part becomes vertically inclined. There are five distinctly impressed pleural furrows which are best marked at their mid-length and almost reach lateral margin. Interpleural furrows are fractionally longer than pleurals, deepest distally, become very faint proximally though are never completely effaced. Fifth interpleural furrow runs on outside of an exsagittally directed ridge which probably represents anterior pleural band of sixth pleura and confines (abaxially) the postaxial sector. Inside this ridge is a very shallow furrow. In lateral profile there is a break in slope between terminal axial piece and postaxial sector. Border rolls under at lateral margin, is widest (tr.) anteriorly.

Ornament on glabella and fixed and free cheek inside posterior and lateral borders consists of tubercles and pustules of many different sizes which are close together. Abundance of tubercles falls off towards furrows; tubercles absent in deepest part of axial furrow, preglabellar furrow, lateral and posterior border furrows and occipital furrow. Tubercles are closely packed and more uniform in size on outer side of anterior border, lateral border, rostral plate, central part of pygidial axis, distal posterior margins of pleurae, outer pleural region and border roll of pygidium; on posterior part of lateral border roll tubercles are more elongate; on cephalic and pygidial borders tubercles are more flattened. Much more widely scattered fine tubercles on thorax, except for pleural, axial and articulating furrows. Pleural facets have fine granules. On inner part of pygidial pleural region and abaxial part of pygidial axis tubercles are scarce. Closely spaced fine tubercles and granules on hypostome except for maculae.

DISCUSSION. Calymene blumenbachii was last described in 1933 (Shirley), though since it was founded (1822) it has probably been more frequently cited than any other calymenid. A full synonymy list would run the length of several pages and the one presented here is of selected references.

The characters which combine to distinguish the species are given in the diagnosis; of particular note is the very narrow, raised, sharply edged anterior border and the highly inflated, anteriorly and dorsally projecting glabella. There is variation in the outline of the glabella and particularly in the outline of the frontal lobe (noted also by Shirley). Four specimens of approximately equal size are illustrated here to show the range of this variation. At one end of the series GSM 19688 shows a strongly bell-shaped glabellar outline with a very rounded frontal lobe, at the other extreme BU 413 (Hollcroft Colln.) has a weakly bell-shaped glabella and the frontal lobe is almost straight.

The syntype of Brongniart figured by Shirley (1933, pl.1, figs. 1,2) agrees best with BM 44213 and BU 283 (Hollcroft Colln.), two specimens intermediate in glabellar morphology. All four specimens are near identical in other features and can only be regarded as conspecific. Minor variations include the degree to which the extreme posterior part of the facial suture turns outward at the genal angle, the presence or absence of a 4p lobe and the number of pygidial axial rings.

Calymene lata Shirley, 1936 from the Wenlock Limestone of Dudley is here considered a junior synonym of *C. blumenbachii*. The characters on which *lata* was established were its "large size, relatively wide glabella, and short upturned preglabellar field" (Shirley 1936, p. 415). The holotype of *lata* (SM A3325) is very large (glabellar width 24.0mm), but the length to width ratio of its glabella (1:1) and its glabellar outline both come within the range of variation here accorded to Brongniart's species. The glabellar outline falls towards the strongly bell-shaped end of the series given above; evidence from other Dudley specimens of equivalent size suggests this shape is characteristic of large *blumenbachii* specimens. The preglabellar area of the holotype of *C. lata* is fractionally less upturned than that of typical *blumenbachii* cranidia but this is not taken as significant. The holotype shows a few other differences from smaller individuals - such as a deeper, more V-shaped lateral border furrow, slightly coarser ornamentation, and very much narrower axial furrows around lobe 1p, but I prefer to regard these as ontogenetic rather than interspecific distinctions. R. & E. Richter (1954, p. 19) were of the same opinion. Certainly the small specimen (SM A3322) of *C. lata* figured by Shirley (1936, pl. 30, fig.12) can in every respect be compared with *C. blumenbachii*.

Calymene ceratophthalma Woodward,1868 from the Wenlock Limestone of Dudley was established on the basis of one specimen which appeared to have long horns projecting from the palpebral lobes. This specimen was subsequently lost trace of but Dr. P. Lane (Univ. of Keele) kindly informed me that it is now housed in the Wollaton Hall Natural History Museum, Nottingham. The so-called "eye peduncles" are in fact the ventral sides of the lateral border of a second cephalon which has turned upside down and slotted into the first specimen. C. ceratopthalma is in all features the same as blumenbachii and is therefore placed in synonymy.

The two most closely related species to blumenbachii are C. clavicula Campbell, 1967 from strata of probable upper Wenlock or lower Ludlow age in Oklahoma, and C. neotuberculata Schrank, 1970 from the upper Wenlock of Gotland. Campbell recognised that clavicula and blumenbachii were strongly allied but differentiated the American species on some eleven characters. The more obvious of these include the coarser glabella ornament, less steeply inclined palpebral lobes, deeper lateral border furrow and occipital furrow, slight pygidial cincture, shorter pleural and interpleural furrows - the latter being much less pronounced, and the larger median spine on the hypostome. One may add that in clavicula the margin of the hypostome between the posterior spines is U-shaped. Contrary to Campbell's claim, in clavicula the posterior spines of the hypostome appear relatively shorter, and the occipital ring relatively longer than in blumenbachii. Although the differences outlined are fairly numerous, many of them concern fine detail, and the American and British species are very closely matched.

A comparison of blumenbachii with neotuberculata is given below.

Tomczykowa (1957, p. 135) has recorded C. blumenbachii blumenbachii and erected C. blumenbachii bardensis from the Wenlockian of the Holy Cross Mountains. Schrank (1970, p. 137) recognised that blumenbachii bardensis was founded on very small (? meraspid) cranidia, that the diagnostic characters of this subspecies (e.g. genal spines, almost parallel sided glabella) are shown by all immature calymenid cranidia, and that the specimens of blumenbachii bardensis may represent juvenile stages of the species Tomczykowa identified as blumenbachii blumenbachii. The Polish specimens have been flattened and cannot be accurately compared with the well preserved topotype specimens of blumenbachii, but the one holaspid cranidium figured (Tomczykowa 1957, pl. 3, fig. 3) seems to have a much more stoutly developed anterior border than in the British species. More significantly it is uncertain, from this figure, whether or not the Polish species has a genal buttress to lateral lobe 2p.

OCCURRENCE. Specimens which with certainty can be referred to this species have been recorded by the present author only from the Wenlock Limestone of the South Staffordshire Silurian inliers.

Calymene neotuberculata Schrank, 1970

Plate 31, figs. 1-9.

1885 Calymmene tuberculata BRÜNNICH; Lindström p.63, pl. 16, fig. 9.

1970 Calymene blumenbachi neotuberculata subsp. n.; Schrank, p. 134 pl. 8, figs. 1-5, pl. 9, figs. 1-4. (Includes a more complete synonymy list).

HOLOTYPE. Well preserved incomplete cranidium; MB Q.K. 1.37 p.233; figured Schrank 1970, pl. 8, figs. 1, 1a.

TYPE STRATUM AND TYPE LOCALITY. Silurian, Gotland. Further particulars unknown (after Schrank 1970, p. 135).

ADDITIONAL MATERIAL. Twelve cranidia, RM Ar6213-17, RM Ar27360, RM Ar27364, RM Ar27458, RM Ar31440, RM Ar47825, RM Ar47848, RM Ar47852; four pygidia, RM Ar27349, RM Ar27462-463, RM Ar31439.

DIAGNOSIS. See Schrank 1970, p. 135.

DESCRIPTION. See Schrank 1970, pp. 135-136.

DISCUSSION. Lindström (1885) and other early Scandinavian authors regarded Calymene tuberculata (Brünnich, 1781) as a senior synonym of C. blumenbachii. However, Shirley (1933, p. 52) examined the type material of tuberculata and concluded that none of the calymenid specimens were well enough preserved to be referred " to any of the species recognised as occurring at Dudley, the type locality", and consequently "the name tuberculata for any species of Calymene must be allowed to fall". At the same time Shirley (1933, p.62) noted that non-type material from Scandinavia which had been referred to tuberculata showed differences from specimens of C. blumenbachii Brongniart. Schrank (1970) has since recognised these differences to be constant, and established C. blumenbachii neotuberculata.

C. blumenbachii neotuberculata was differentiated from blumenbachii blumenbachii by its sagittally longer anterior border which is more convex in lateral profile and less close to the frontal glabellar lobe, and its 1p lobe in which the anterolateral corner more closely approaches the fixed cheek. Excellently preserved material of neotuberculata figured here is identical with the holotype, can be accurately compared with blumenbachii blumenbachii material from Dudley, and the following points of distinction supplement those given by Schrank: A more incised occipital furrow behind the median lobe; slightly more flattened and less steeply sloping preocular part to the fixed cheek; less transversely convex, upstanding glabella, the frontal lobe of which is not undercut by the preglabellar furrow; much weaker furrow between the fixed cheek and anterior border. These differences are considered sufficient to elevate neotuberculata to specific rank.

A small holapis of neotuberculata (RM Ar6213) shows a less bell-shaped glabella and wider axial furrow outside lobe 1p than in more adult cranidia. In the latter respect this small holaspis is similar to blumenbachii, but it clearly still has a much broader (sag.) convex anterior border than the English species. Evidently in both neotuberculata and blumenbachii the axial furrow outside lobe 1p becomes narrower during ontogeny (see discussion of blumenbachii), but there is no doubt that in 'average' (glabellar width around 10.0mm) sized adults of both species it is narrowest in neotuberculata (compare RM Ar273[illegible] with BU 413). The outline of the frontal glabellar lobe in neotuberculata varies from moderately convex to almost straight, as in blumenbachii (compare RM Ar31439 with RM Ar27364).

Schrank (1970, p. 137, pl. 10, fig. 5) differentiated an unnamed subspecies of C. blumenbachii on the basis of one cranidium from the Wenlockian of Estonia; in its synonymy he placed the material which Schmidt (1894, p.13, pl.1, figs. 1-8; 1907, p. 53, pl. 3, figs. 1, 1A) had referred to C. tuberculata Brünnich. The status of this taxon cannot be fully assessed until the Baltic material has been revised, though it appears to be closer to neotuberculata than blumenbachii.

C. clavicula Campbell, 1967 is distinguished from neotuberculata by its straighter anterior cranidial margin, slightly narrower (sag.) anterior border which is more swollen opposite the axial furrow, sagittally narrower preglabellar furrow, shorter and distally weaker interpleural furrows, and shorter pleural furrows (see Campbell 1967, pl. 9, figs. 9, 12).

OCCURRENCE. Schrank gave the range of neotuberculata on Gotland as from the Högklint Beds (= lower Wenlock) to the Mulde Beds (= upper Wenlock). All the specimens I have examined are from the Mulde Beds in the parishes of Eksta (at Djupvik) and Fröjel, where it is accompanied by C. tuberculosa Dalman, and C. falcata sp. nov.. Also recorded from Graptolithengestein erratics of N Germany.

Calymene cf. C. neotuberculata Schrank, 1970

Plate 30, figs. 4-6.

MATERIAL. One incomplete cranidium and its counterpart, GSM 103182-183.

OCCURRENCE. Lower Ludlovian, scarp 80 yards S., 30° W. of Brynsyllдy Farm, Llanwrst, Denbighshire.

DISCUSSION. This species shows affinities with C. blumenbachii and C. neotuberculata though it also shows some resemblance to C. lawsoni Shirley, 1962 (compare with LE 589A). It differs most obviously from lawsoni in having a narrower (exs.) posterior border furrow, the lack of a paired arrangement of tubercles on the median glabellar lobe, and a very weak inflation of the anterior border opposite the fixed cheek. The form of the anterior border and the axial furrow around lobe 1p distinguish the Welsh cranidium from C. blumenbachii specimens of a similar size, and place it close to C. neotuberculata with which it is here compared.

Calymene tenera Barrande, 1852

Plate 32, figs. 1, 2, 4-8, 10, 11.

1852 Calym. tenera Barr.; Barrande, p. 574, pl. 19, figs. 26, 27.

1970 Calymene? tenera Barrande; Marek in Horny & Bastl, p. 309.

1970 Calymene (Diacalymene) tenera Barrande; Schrank, p. 126.

LECTOTYPE. Designated Marek in Horny & Bastl 1970, p. 309; an incomplete cranidium with the cuticle partially remaining; NMP It346, CE 1252; figured Barrande 1852, pl. 19, fig. 26, and here Pl. 32. figs. 1, 2, 4, 8.

TYPE STRATUM AND TYPE LOCALITY. Kopanina Formation, horizon with <u>Cromus</u> <u>beaumonti</u> (= lower Ludlow in age), Jarov (Dlouha hora), Bohemia.

PARALECTOTYPE. A poorly preserved pygidium; NMP It347; figured Barrande 1852, pl. 19, fig. 27, and here Pl. 32, figs. 5, 6.

ADDITIONAL MATERIAL. (At hand). One pygidium, NMP unnumbered.

DIAGNOSIS. Axial furrow narrow around lobe 1p, about three times as wide as this at lobe 3p. Preglabellar area about $^1/5$ as long as glabella; shallow preglabellar furrow about $^1/8$ as long as glabella. Anterior border mildly convex (sag. & exs.). Pygidium has six short pleural furrows, slightly longer and extremely weak interpleurals, wide border, at least nine axial rings.

DESCRIPTION. Glabella bell-shaped in outline, about as wide as long. Occiptial ring narrows abaxially; occipital furrow deepest behind lateral lobe 1p. The latter is large, subquadrate, one third as wide as glabella, has a moderately convex outer margin and pointed antero-lateral corner, is separated from median lobe by shallow furrow. Lateral furrow 1p very narrow between first two lateral lobes, directed inwards and slightly backwards, bifurcates at median lobe, longer posterior branch directed more backwards, anterior branch runs forwards and inwards across neck of lobe 2p. Small intermediate lobe within fork of furrow 1p. Elongate lobe 2p trends outwards and slightly forwards, is joined abaxially to rather small genal buttress and is independently convex of median lobe. Furrow 2p transversely directed, rather narrow and deep. Glabellar outline narrows sharply in front of lobe 2p. Lateral lobe 3p on dorsolateral glabellar surface, directed transversely, quite strongly swollen, confined anteriorly by well marked furrow 3p. No 4p lobe indicated on lectotype. Anterolateral corners of frontal lobe quite sharply rounded, anterior margin moderately convex forwards and projects slightly in front of fixed cheek. In lateral profile occipital ring stands higher than dorsal surface of median lobe. The latter is gently convex and anteriorly falls progressively more steeply to frontal lobe, thereafter descending very steeply to preglabellar furrow.

Axial furrow very narrow around lobe 1p, much wider at furrow 1p, between furrow 2p and preglabellar furrow it is widest and about three times as wide here at at lobe 1p. Deep anterior pit sited on inner side of base of axial furrow half-way along the side of frontal lobe. Preglabellar furrow very shallow and rather long (sag. & exs.), rises very gently to anterior border. Anterior border does not reach above base of frontal lobe, is mildly convex (sag. & exs.) and wider opposite axial furrow than at median line; outer side of border falls downwards and forwards to rostral suture. In dorsal view anterior margin is weakly arcuate, in frontal view rostral suture is very weakly convex upwards. In lateral profile preocular part of fixed cheek is substantially more convex and steeply sloping than postocular part. Outer part of fixed cheek and posterior branch of facial suture unknown. Anterior branch of facial suture trends forwards and very slightly inwards to anterior margin.

Free cheek, rostral plate, hypostome and thorax unknown.

Pygidium about twice as wide as long, in dorsal view posterior outline is rather pointed at median line. Axis less than one third the total width, tapers gradually posteriorly, in lateral profile its dorsal surface is broadly arched. There are at least nine axial rings and a rather sharply rounded terminal axial piece. Ring furrows shallowest sagittally, deeply incised near axial furrow. Ninth ring furrow almost completely effaced medially, and does not quite reach axial furrow; very faint trace of tenth ring furrow on central part of terminal axial piece. Side of axis becomes progressively more steep posteriorly. Axial furrow very shallow, noticeably expands in width (tr.) behind seventh ring furrow, is lacking behind terminal axial piece. Pleural region descends fairly steeply from axial furrow, becomes vertical then curves slightly under near lateral margin. Six well marked pleural furrows fall well short of lateral margin. Interpleural furrows are only slightly longer than pleurals and almost obsolete. There is a wide smooth border on outer side of pleural region. Weakly defined (abaxially) postaxial sector is continuous (in lateral profile) with terminal axial piece, and falls nearly vertically to posterior margin.

Ornament of cranidium unknown. Outer part of pleural region of pygidium covered with very small tubercles.

DISCUSSION. Calymene tenera represents the earliest known Calymene from the Bohemian succession and has not been revised since it was founded in 1852, though Marek (in Horny & Bastl 1970) has recently selected a lectotype for the species from one of Barrandes figured specimens. The species is not common, and I have only the type cranidium and two pygidia at hand. A Calymene cranidium (DJS/129) collected by the present author from the Kopanina Formation is very similar to the lectotype of tenera, yet differs in having a concave outline to the frontal lobe and no intermediate lobe within the fork of 1p furrow; consequently this cranidium is here only questionably referred to tenera, but may well be assigned with certainty when the range of variation of Barrande's species is known. It is assumed that the isolated syntype (now paralectotype) pygidium which Barrande illustrated under C. tenera does, in fact, belong to this species. The hypostome of C. tenera is said to be unknown, but it is possible that the hypostome described elsewhere by me as Metacalymene baylei? (Barrande, 1846) belongs to C. tenera, as both species occur in the Kopanina Formation.

C. tenera is easily distinguished from the later C. interjecta, the only other named Bohemian Calymene, by its longer preglabellar area, longer preglabellar furrow, more convex anterior border, and greater number of axial rings and pleural furrows on the pygidium. Apart from the latter character, the pygidium of tenera is noticeable for its axis, which in lateral profile is broadly arched along the median line. This feature has also been observed in C. spectabilis and some specimens of C. interjecta and C. tentaculata campana. The overall form of the pygidium in C. tenera is perhaps closest to that of C. spectabilis, though in detail they can be distinguished, and the cranidia of the two species are very different.

C. tenera is probably most closely related to C. tentaculata Schlotheim, 1820, and its cranidium almost falls within the range of variation accorded to tentaculata by Schrank (1970, p.139), except it has a much narrower axial furrow around lateral lobe 1p. Of the four main types of cranidium discerned in tentaculata (see below), that of tenera is intermediate between variants 1 and 2, and appears closest to the cranidium figured by Schrank (1970) on pl. 11, fig. 4. The pygidium of tentaculata differs from that of tenera in having only five pleural furrows and eight axial rings, longer pleural furrows, longer and abaxially deeper interpleural furrows, and no border. C. tentaculata campana subsp. nov. is immediately differentiated from tenera by its sagittally shorter preglabellar furrow.

The cranidium of C. neotuberculata has a shorter and deeper preglabellar furrow, a narrower axial furrow in front of lobe 2p, a more upstanding anterior border and a less convex (tr. & exs.) preocular part to the fixed cheek. C. tenera can be more closely allied to tentaculata than to neotuberculata.

OCCURRENCE. Known only from the Kopanina Formation in the vicinity of the type locality (Dlouha hora), Bohemia.

Calymene tentaculata (Schlotheim, 1820) campana subsp. nov.

Plate 33, Figs. 1-8; Plate 34, figs. 1-6.

1909 Calymmene intermedia Lindstr.; Moberg & Grönwall (pars), p. 71, pl. 3, figs. 15, 16.

? 1970 Calymene sp. aff. blumenbachi neotuberculata et tentaculata; Schrank, p.138, pl. 9, fig. 7, pl. 10, figs. 1-4.

DERIVATION OF THE NAME. From the latin, campana, bell, referring to the very strongly bell-shaped outline of the glabella.

HOLOTYPE. Complete cranidium; RM Ar32803; Pl. 33, figs. 3-6.

TYPE STRATUM AND TYPE LOCALITY. Loose block of upper Silurian age (no older than topmost Whitcliffian), Ramsåsa district, Scania. It is unknown whether the holotype originated from the in situ upper Silurian of Scania or was transported into the district within a glacial erratic (see occurrence).

ADDITIONAL MATERIAL. Six cranidia, RM Ar27767, RM Ar32801, RM Ar32803, RM Ar32959, RM Ar32961-962; seven pygidia, RM Ar32800, RM Ar32802, RM Ar32807, RM Ar32809, RM Ar32950, RM Ar32952, RM Ar32958; one thoracic segment, RM Ar32804.

DIAGNOSIS. Subspecies of C. tentaculata with very strongly bell-shaped glabella; conspicuously swollen intermediate lobe at adaxial end of furrow 1p; well defined anterior branch to furrow 1p; very narrow (tr.) median lobe between the long, deeply incised posterior branches of furrow 1p; long, fairly convex (sag.) anterior border.

DESCRIPTION. Cranidium about twice as wide as long. Glabella is 1.0 - 1.1 times as wide as long, very strongly bell-shaped, projects in front of fixed cheek. Occipital ring is widest at sagittal line and begins to narrow immediately from here to occipital furrow; in profile it is very weakly convex. Occipital furrow moderately deep and wide at median line, is directed outward and backward from here to axial furrow; behind lobe 1p it is deep. Lobe 1p is large, subquadrangular in outline and more than one third as wide as glabella, connected to median lobe by very narrow (exs.) neck. Furrow 1p very long (tr.), deepest abaxially, runs inwards and backwards and bifurcates at median lobe; deeply impressed posterior branch curves a little more backward then sharply inward; anterior branch is well marked, runs inward then forward to isolate lobe 2p from median lobe. Very distinct intermediate lobe at adaxial end of furrow 1p. Lobe 2p elongate, directed outward and slightly forward as is the deep lateral furrow 2p. Lobe 3p about the same size as intermediate lobe, transversely elongate, prominently swollen. Very small 4p lobe and 4p furrow also present. Frontal lobe very short (sag.) - about four and a half times as wide as long and only 0.6 times as wide as glabella at lobe 1p; anterolateral margins rounded, anterior outline is straight (tr.) or very gently arcuate. Median lobe of glabella extremely narrow (tr.) at occipital furrow, widens considerably anteriorly. In lateral profile dorsal surface of glabella projects moderately above fixed cheek, falls progressively more steeply as it runs forward from lobe 2p to preglabellar furrow, though does not become vertically inclined on anterior face of frontal lobe.

Axial furrow very shallow at occipital furrow, deep and moderately wide outside middle of lobe 1p, narrows at anterolateral corner of lobe 1p, widest at furrows 1p and 2p, narrows slightly from furrow 2p to anterior pit which is sited just in front of furrow 4p. Preglabellar furrow moderately shallow, about as wide as axial furrow at 4p lobe, fractionally undercuts frontal lobe. Furrow between fixed cheek and anterior border is of the same width as preglabellar furrow though slightly shallower, runs outward and backward. Anterior border about twice as wide as preglabellar furrow at median line, about three times as wide (exs.) opposite axial furrow where it is extended posteriorly; in section (sag.) it is fairly convex, and rolls smoothly over from preglabellar furrow to its outer side which descends slightly forwards to rostral suture. In frontal view the latter is almost straight. In dorsal view anterior margin is gently arched.

Postocular part of fixed cheek is about 0.9 times as wide as occipital ring. Posterior border furrow widest (exs.) half-way between axial furrow and facial suture. Palpebral lobe is slightly longer (exs.) than lobe 2p but not as long as lobe 1p, centred opposite lobe 2p. In frontal view fixed cheek continues the slightly downward and inward slope of the palpebral lobe towards the genal buttress; preocular part of fixed cheek is a little flattened, inclined downwards and forwards, postocular part less steeply inclined. Posterior branch of facial suture runs outwards then backwards to lateral border where it turns more sharply backwards to posterior margin; anterior branch trends forwards and inwards.

Pygidium about 1.8 times as wide as long. Axis about one third as wide as pygidium, has eight axial rings, and a bluntly rounded terminal axial piece, in section (tr.) is quite strongly convex and in lateral profile extremely weakly arched (sag.). Each ring furrow is deepest abaxially, eighth ring furrow is effaced medially. Inner part of pleural region slopes steeply downward, outer part is vertically inclined. There are five deeply incised pleural furrows which become slightly wider (exs.) abaxially and do not quite reach lateral margin. Interpleural furrows slightly longer than pleurals, rather broad but quite distinct abaxially, narrow rapidly towards axis, seemingly absent on innermost part of pleural region. Axial furrow sharply impressed along the sides of the axis, almost lacking between terminal axial piece and postaxial sector.

Ornament on glabella, anterior border, and fixed cheek in front of posterior margin of palpebral lobe consists of rather fine, fairly closely spaced tubercles and granules. Tubercles become more widely scattered on abaxial part of fixed cheek. Anterior slope of posterior border furrow has a few fine tubercles. Closely spaced tubercles on outer part of pygidial pleural region and central part of axis. Lateral glabellar, axial and preglabellar furrows are lacking in ornament. Tubercles on the smallest specimen (RM Ar32961) are relatively larger.

DISCUSSION. The overall morphology of the cranidium and pygidium, and the fine cranidial tubercles immediately identify this Swedish material with C. tentaculata (Schlotheim). Schrank (1970a, p. 575) has recently rehabilitated this species which was founded on the basis of a cranidium in a Beyrichienkalk (Downtonian in age) erratic from N Germany; the holotype was refigured (pl. 3, fig. 2) together with other material from the upper Silurian of the Leba 1 borehole in Pomerania that was regarded as conspecific. In another paper Schrank (1970, p.138) assigned many specimens from Beyrichienkalk erratics to tentaculata. The unavailability of in situ "topotype" material of tentaculata results in a more arbitrary limitation of the morphological variation of this taxon, than is normal for most Calymene species. Schrank adopted a wide interpretation, the morphology of the specimens from the Leba borehole and Beyrichienkalk erratics showing appreciable variation, especially with respect to the preglabellar area. Four main types of preglabellar area were recognised (Schrank 1970, p. 139):

1) A fairly flat anterior border which runs smoothly posteriorly into the preglabellar furrow.

2) A higher anterior border which has a slight edge against the preglabellar furrow.

3) A roll-like anterior border which lies fairly close to the glabella

4) A very high, erect anterior border combined with a very long preglabellar furrow.

C. tentaculata campana is quite distinct from those specimens of tentaculata illustrated by Schrank which have the first or fourth type of anterior border,and which themselves probably merit separate sub-specific rank from the nominate subspecies (see Schrank 1970, pl. 11, fig. 6, pl. 12, fig. 3; 1970a, pl. 1, pl. 2, figs. 1, 2.). C. tentaculata campana has a similar type of preglabellar area to that of the poorly preserved holotype of C. tentaculata tentaculata, which corresponds to type three above; a slightly better preserved N German cranidium of this type was figured by Schrank (1970) on pl. 11, fig. 1. The new sub-species, however, shows the following points of distinction: A much more strongly bell-shaped glabella; a considerably more swollen, discrete intermediate lobe at the adaxial end of furrow 1p; a better defined anterior branch to furrow 1p; a narrower (tr.) median lobe between the long, well incised posterior branches of furrow 1p.

There is minor variation in tentaculata campana. The single cranidium from Gotland (RM Ar27767; see occurrence) shows slight differences from the Scanian cranidia - in having more steeply inclined palpebral lobes, a more sagittally convex anterior border and a marginally deeper preglabellar furrow, but they are all treated here as belonging to the same taxon.

Schrank (1970, pl. 10, figs. 6, 6a) has refigured original material of Calymene beyeri R. & E. Richter, 1954 from the Köbbinghauser Beds of the Rhineland and placed it in the synonymy of C. tentaculata. C. beyeri is here considered a junior synonym of C. tentaculata tentaculata.

Calymene kokbaitalensis Maximova, 1968 and C. weberi Maximova, 1968 from the upper Silurian and lower Devonian of Kazakhstan are closely related to C. tentaculata (Schrank 1970, p. 140). Both species (especially kokbaitalensis) show great resemblance to tentaculata campana in the form of the glabella, lateral furrow 1p and intermediate lobe, but kokbaitalensis differs in having a relatively longer preglabellar furrow and longer preglabellar area, and weberi has a shorter, angular (sag.), more upturned anterior border, and a notch in the outer wall of the axial furrow opposite furrow 2p.

The succession and morphology of certain Calymene taxa on Gotland sustains the suggestion (Schrank 1970, p. 136) that C. tentaculata is on a line of descent from C. neotuberculata. Of the characters which serve to differentiate these two species, ornamentation is the most constant, C. tentaculata having glabellar tubercles which are smaller and less variable in size.

OCCURRENCE. All the Swedish specimens of this taxon are from Scania except one cranidium (RM Ar27767) which is from Gotland.

The latter cranidium is labelled as coming from the parish of Sundre in which both the Hamra and Sundre Beds outcrop; these are the youngest supramarine Silurian deposits on Gotland and are both correlated with the upper Whitcliffian (Cocks et al. 1967, fig. 9).

The Scanian material comes from loose slabs of a red limestone collected from the Ramsåsa district. There is no label information to indicate whether these slabs are from the in situ upper Silurian of this area or if they are derived from elsewhere. However, Moberg & Grönwall (1909) figured a Calymene from the Upper Öved Ramsåsa Beds (= Downtonian in age) which is here regarded as conspecific with C. tentaculata campana, and this suggests the former alternative to be more likely. Concomitant beyrichiacean ostracodes in the limestone blocks include species of Lophoctenella, Neobeyrichia, Hemsiella and Berolinella (identified by David J. Siveter). Berolinella is not found in the supramarine sequence on Gotland and the two named species of this genus are from N German Silurian erratics of post Whitcliffian age (see Martinsson, 1962, pp. 253, 254; 1967, p. 376).

Calymene sp. 2

Plate 34, figs. 7-11.

MATERIAL. One internal mould cranidium and its counterpart, GSM RK3991-992; one external mould pygidium, GSM RK3987.

OCCURRENCE. Lower Ludlovian (scanicus zone?), small quarry 390 yards N at 57° E from Graig - bach, Denbighshire. (Nat. Grid. Ref. SH[illegible]56125).

DESCRIPTION. Glabella bell-shaped in outline. Lateral lobe 1p large and very wide, is joined to median lobe by very narrow (exs.), wide 'neck'. Lateral furrow 1p is deeply incised, bifurcates adaxially and confines a most conspicuous intermediate lobe. Median lobe is extremely narrow (tr.) between the very long posterior branches of furrow 1p. Anterior branch of furrow 1p clearly divorces the elongate lobe 2p from the median lobe. Lateral furrow 2p is deep; lobe 3p is strongly inflated and like the intermediate lobe is stretched down the side of the glabella. Furrow 3p quite distinct. Small 4p lobe and 4p furrow present low down on glabella side. Frontal lobe projects in front of fixed cheek, its anterior outline is concave forwards.

Axial furrow is very deep, outer wall is slightly concave immediately in front of genal buttress, opposite lobe 4p outer wall trends inwards. Preglabellar furrow very deep. Posterior side of anterior border runs steeply and smoothly upwards from preglabellar furrow, dorsal side turns sharply over to run downwards and backwards to rostral suture. Opposite axial furrow posterior side of anterior border is quite strongly swollen.

Palpebral lobe centred opposite anterior margin of lobe 2p. As far as can be determined ornament of glabella, fixed cheek and anterior border consists of rather fine tubercles.

DISCUSSION. This species can not be readily allied with any other Calymene in the British Silurian. The lp lobe, lp furrow, intermediate lobe, median lobe between lp furrows, and anterior border opposite the axial furrow are more comparable with those in the Russian and Baltic species, C. kokbaitalensis, C. weberi, and C. tentaculata campana (see description and previous discussion). The anterior border of Calymene sp. 2 is not dissimilar to that of C. weberi (= C. aff. weberi of Maximova, 1968; see Schrank 1970, p. 740), but it is more upward and inwardly curved in the latter, which in addition does not have a concave outline to the frontal lobe.

The Welsh species is possibly new, and represents an interesting connection with these later Silurian and early Devonian taxa. An attempt by the present author at collecting additional material met with no success.

Calymene lawsoni Shirley, 1962

Plate 35, figs. 1-10; Plate 36, figs. 1-11.

1954 Calymene Calymene beyeri?; R. & E. Richter, p. 19, pl. 2, figs. 25, 26.

? 1960 Calymene cf. beyeri (Richter); Squirrell & Tucker, p. 177.

1962 Calymene sp. nov.; Whitaker, pp. 345, 348, 350.

1962 Calymene lawsoni sp. nov. (nom. nudum);Shirley, p.237.

? 1967 Calymene cf. beyeri Richter; Phipps & Reeve, p. 367.

1968 Calymene lawsoni; Shergold & Shirley, p. 135.

1968 Calymene lawsoni Shirley (nom. nud.); Haas, pp. 98, 99, text-fig. 16e, 16f.

SYNTYPES. Two internal moulds of incomplete cranidia; SMF 1652a, figured R. & E. Richter 1954, pl. 2, fig. 25, and SMF 1652b, figured R. & E. Richter 1954, pl. 2, fig. 26. Other syntypes include those specimens on loan from Dr. J.H. McD. Whitaker (Univ. of Leicester) to Dr. J. Shirley (see discussion and Shirley 1962, p. 237).

TYPE STRATUM AND TYPE AREA. Leintwardine Stage, Ludlow Series, Leintwardine area and Park Farm, S end of Wenlock Edge near the R. Onny valley, Welsh Borderland.

ADDITIONAL MATERIAL. About fifty cranidia, fifty pygidia and fifteen hypostomes. In addition there are numerous fragments and many isolated thoracic segments. All of the material is in the form of either internal or external moulds and comes from the Leintwardine collections of Dr. J.H. McD. Whitaker.

DIAGNOSIS. Species of Calymene with straight (tr.) or weakly convex outline to the anterior margin and the frontal lobe (in dorsal view). Gently convex (sag.), weakly inflated glabella. No distinct intermediate lobe at inner end of furrow 1p. Fixed cheek falls fairly gently (exs.) from palpebral lobe. Posterior border furrow wide (exs.). Linear (exs.) and paired (tr.) arrangement of large perforate tubercles on frontomedian glabellar lobe, inner part of fixed cheek, and pygidial axis. Six to seven axial rings, five pleural furrows.

DESCRIPTION. Cephalon about two and one third times as wide as long. Dorsal surface of occipital ring moderately convex (sag. & exs.), falls very steeply into occipital furrow, narrows quite sharply behind 1p lateral lobe towards axial furrow. Occipital furrow V-shaped and quite deeply incised across central area of glabella, becomes deeper and narrower abaxially. Glabella is bell-shaped, slightly longer than wide, projects fractionally in front of fixed cheek; in lateral profile it is horizontal from occipital furrow to furrow 2p, then falls gently to the anterior margin of the frontal lobe and finally vertically into the preglabellar furrow. Width of glabella at 1p lobes is about one and a half times that across frontal lobe.

Subquadrate lobe 1p is just less than one third as wide as glabella, separated from median lobe by shallow furrow, has a somewhat pointed anterolateral corner. Lateral furrow 1p rather deep and very narrow between 1p and 2p lobes, bifurcates at median lobe, the posterior branch turning more backwards and finally running transversely, a short anterior branch being directed forwards and inwards around inner neck of lobe 2p. Glabella sometimes gently swollen within fork of furrow 1p but no discrete intermediate lobe present. Lobe 2p subcircular or elongate with its long axis trending gently forwards and outwards. Furrow 2p runs inwards and slightly backwards. Node-like lobe 3p is slightly elongate (tr.); furrow 3p distinct. Many specimens have a very small 4p lobe and extremely weak 4p furrow. Subrectangular frontal lobe is three and a half to four times as wide as long, anterior margin straight (tr.) or very weakly convex forwards.

Axial furrow very shallow at occipital ring, is narrowest around posterior part of lobe 1p, deepest at furrows 1p and 2p. Some specimens show very weak trace of eye ridge on abaxial side of axial furrow opposite furrow 3p. Anterior pit sited in axial furrow below or just anterior to 4p lobe. Preglabellar furrow rather short (sag. & exs.), moderately deep, its anterior slope rises steeply (less so in small specimens) to convex or somewhat angular (sag.) anterior border. Anterior margin is straight (tr.) or very weakly arched forwards.

Posterior border widens gradually from axial furrow to fulcrum, expands (exs.) more quickly from fulcrum to facial suture. Posterior border furrow rapidly expands in width abaxially, is very wide half-way between axial furrow and genal angle, does not quite reach facial suture, anterior slope is much less steeply inclined than posterior slope. Postocular part of fixed cheek very gently inclined between palpebral lobe and posterior border furrow; preocular part of cheek slightly more steeply sloping and a little more convex. Palpebral lobe centred opposite anterior margin of lobe 2p, is almost as long as lobe 1p, projects outwards and moderately upwards from fixed cheek. Posterior branch of facial suture runs outwards from palpebral lobe before turning posteriorly to cross lateral border furrow, then turns sharply backwards to genal angle. Anterior branch trends forwards and inwards to anterior margin.

Free cheek bears narrow eye socle. Lateral border furrow rather broad, especially anteriorly, rises quite sharply to lateral border which rolls over and under to meet reflexed doublure.

Fragmentary rostral plate is of normal calymenid type composed of border and doublure sectors.

Hypostome slightly wider (tr.) than long. Very narrow anterior border is flexed ventrally. Anterior border furrow scarcely impressed, absent abaxially. Anterior wing has deeply incised pit. Lateral border tightly convex (tr.). Lateral border furrow quite distinct. Posterior border expanded into two short spines. Posterior border furrow sharply incised and transversely directed. Median furrow most distinct where it merges with lateral border furrow, fades very quickly towards ovate weakly convex macula, hardly perceptible medially. Anterior lobe three and a half to four times as long as posterior lobe, bears a very prominent spine near its centre. Posterior lobe crescent-shaped, its sides are long (exs.) and drawn forwards to a point opposite (tr.) median spine.

Axis of pygidium about one third total width of pygidium, tapers gradually posteriorly, its sides become more steeply inclined towards terminal axial piece, it has six to seven axial rings. At least first four ring furrows are complete, fifth sometimes complete, sixth and seventh only present abaxially. All ring furrows most deeply incised at axial furrow. Terminal axial piece well rounded. Axial furrow weakest posteriorly. There are five well marked pleural furrows which are most strongly impressed abaxially and fall well short of lateral margin. Interpleural furrows are very weak on inner half of pleural region, become more distinct abaxially, are longer than pleural furrows and almost reach lateral margin. Fifth interpleural furrow forms side of postaxial sector which is limited either side median line by a ridge which runs exsagittally from near junction of sixth ring furrow and axial furrow. Pleural furrows more distinctly impressed than interpleurals.

Except in preglabellar and axial furrows cranidium is covered with small to medium sized tubercles. In posterior border furrow tubercles more widely spaced. On frontomedian glabellar lobe there are two parallel rows (exs.) of larger, perforate tubercles which show a paired (tr.) arrangment. Along each row the tubercles are in approximately the following positions: On occipital ring one third of its width (tr.) in from axial furrow; near inner neck of lobe 1p; opposite (tr.) posterior margin of lobe 2p; opposite adaxial part of furrow 2p; opposite adaxial part of furrow 3p; opposite lobe 4p. On one specimen (LE 589a) a further perforation is seen on occipital ring either side the more central pair, and a possible linear (tr.) arrangement of pits on posterior border as far as fulcrum. There is at least one row (exs.) of four large, perforate tubercles on inner part of fixed cheek running from anterior margin of posterior border furrow to anterior part of part of palpebral lobe; possibly another parallel row in between this one and axial furrow.

Scattered tubercles present all over free cheek - become more flattened and scale-like on lateral border. Inner part of pygidial pleural region almost devoid of tubercles, outer part with very closely spaced small tubercles and granules. Two parallel rows (exs.) of pits on axial rings. Possible linear (tr.) arrangement of pits on posterior pleural bands of inner pleural region.

On internal moulds larger tubercles on glabella and pygidium represented by small spikes of sediment which have infilled the canals in the cuticle. On some casts of pygidia and cranidia larger tubercles are represented only by pits - probably due to abrasion of tubercle rim.

ONTOGENY. Meraspid period. Three cranidia have been recorded which may be meraspides. The length of the glabella in each is 1.2mm (LE 287/5), 1.6mm (MJ 1.132) and 1.9mm (LE 183/4). All of them are poorly preserved internal moulds though one (MJ 1.132) has a counterpart external mould. The glabella in each of the two smaller cranidia is almost parallel sided and there are at least three lateral lobes developed. The larger cranidium (LE 183/4) has a glabella which is more expanded (tr.) at lobe 1p. The two smallest cranidia both have a very long fixigenal spine; the abaxial part of the fixed cheek is destroyed on the largest specimen. All three specimens fail to show the second glabellar lobe in contact with the fixed cheek though the largest specimen (LE 183/4) appears to have the beginnings of a genal buttress. There is a suggestion on the cast of the one external mould(MJ 1.132) that the pairing of the larger glabellar tubercles is already present.

Contact of 2p lobe and genal buttress. Two cranidia (LE 287/1; LE 289/7), both of which have a glabella 2.9mm long, have the 2p lateral lobe in contact with a genal buttress. Both specimens are casts of external moulds. There is one steinkern cranidium (LE 287/2) with a glabella 2.3mm (estimated) long which shows a small genal buttress which may have been in contact with lobe 2p. Taking into account the evidence from the cranidia which are possibly meraspides, it is reasonable to assume the axial furrow was bridged at 2p lobe when the glabella was somewhere between 2.0 and 2.9mm long.

Genal spine. One of the above cranidia (LE 287/1 - glabella 2.9mm long) has the fixed cheek intact and shows no trace of the genal spine that is present on the possible meraspides. The genal spine is therefore lost earlier in ontogeny than that of *C. puellaris* (see ontogeny of that species).

DISCUSSION. *C. lawsoni* has been cited in previous works as a *nomen nudum*, yet all the requirements to make this an available name have been met. In 1954 R. & E. Richter figured two poorly preserved cranidia of *Calymene* (*C.*) *beyeri* ? (= *C. lawsoni*) from the Mocktree Shales (= Leintwardinian in age) of Park Farm at the southern end of Wenlock Edge; these specimens were differentiated by the Richters from their new species *Calymene* (*C.*) *beyeri* on several characters. Shirley (1962, p. 237) later made reference to the Richters publication and to *C.* (*C.*) *beyeri* ? - for which he introduced the new name of *lawsoni*. The date and authorship of *C. lawsoni* therefore stems from Shirley's 1962 paper.

Shirley did not formally designate a holotype, and the syntypes must be regarded as the two cranidia collected by the Richters, together with those specimens from the Leintwardine area which were mentioned by Shirley (1962, p.237) and on loan to him from Dr. J.H. McD. Whitaker (Univ. of Leicester). The restriction of a type stratum (within the Leintwardine Stage) and type locality (either Park Farm or from the Leintwardine area) is dependent on the selection of a lectotype - which is best chosen from the better preserved Leintwardine material. It is hoped this process will be implemented by the author of the species at some future date.

The present author has examined the two syntypes collected by the Richters and is satisfied they are conspecific with the specimens attributed herein to *C. lawsoni*. The latter material is from the Leintwardine collections of Dr. Whitaker and forms the basis for the first detailed account of the species.

Haas (1968, p.99) was in possession of some lawsoni material from the Leintwardine area and suggested the British taxon may be a subspecies of C. arotia, his new species from the upper Ludlovian of N W Turkey. Apart from the fact that lawsoni has priority over arotia, the two taxa are here regarded as specifically distinct. In C. arotia the anterior margin is substantially more arcuate, the anterior border is relatively longer and less steeply upturned, there is a discrete intermediate lobe at the inner end of furrow 1p, the posterior border furrow is much narrower (exs.) and the ornamentation on the glabella is different.

C. orthomarginata Schrank, 1970 from N German erratics of upper Wenlock to lower Ludlow age strongly resembles lawsoni in its very blunt or straight (tr.) outline to the frontal lobe and anterior margin. Also, Schrank (1970, pl. 6, fig. 5) questionably assigned a very small cranidium to orthomarginata, and this cranidium has a linear pattern of large tubercles on the fixed cheek, the same as in lawsoni. But there is no suggestion of the same type of ornament on the glabella of this specimen, or on adult cranidia or pygidia of orthomarginata. Schrank's species differs further through its more depressed slightly shorter glabella, slightly wider (sag.) preglabellar furrow, less vertically directed posterior slope to the anterior border, narrower less convex pygidial axis and a greater number of ring furrows (eight) - the posterior ones of which are much more distinct than those of lawsoni.

C. mimaspera Schrank, 1970 is of the same age as orthomarginata and the two species have been found together in N German erratics (Schrank 1970, p. 129). The cranidial morphology and ornament of mimaspera is quite distinct from that of lawsoni, but at least one pygidium assigned to mimaspera shows a pairing of the larger tubercles on the pygidial axis (Schrank, p. 125, pl. 3, fig. 7). On the basis of this one specimen, mimaspera can be allied with lawsoni.

C. neointermedia and C. puellaris from the Ludlovian of Gotland and Britain also show a paired (though much less obvious) arrangement of tubercles on the posterior part of the median glabellar lobe. As puellaris is associated with lawsoni in the British Leintwardinian, it seems likely that puellaris and neointermedia are close to lawsoni, despite them being easily distinguished from Shirley's species on many other characters.

However, the closest species to lawsoni is C. aff. lawsoni from the British Eltonian and the available material of this species does not show any regular pattern of ornament on the glabella or pygidium (see below).

OCCURRENCE. C. lawsoni is found most abundantly in the Higher Lower Leintwardine beds of the Leintwardine area where it forms part of the fauna inhabiting the six submarine canyon-heads which trend from the shelf margin into the basin. Whitaker (1962) recorded the species from this horizon, and it is also present in the Upper Leintwardine Beds of the Leintwardine area - though more rarely so.

Shergold and Shirley (1968, pl.15) record C. lawsoni from the Upper Bringewood Beds, and Basal and High Upper Leintwardine Beds of Wenlock Edge, the High Lower Leintwardine Beds of the Ludlow area, and the Lower Bodenham Beds and Basal Lower Perton Beds of S. Woolhope. Material from the Upper Leintwardine Beds of Wenlock Edge has been examined (Shergold and Shirley Collection, Brit. Mus. Nat. Hist.) and their recording of C. lawsoni at this horizon corroborated. In biostratigraphical accounts of the Welsh Borderland Silurian, Squirrell and Tucker (1960) and Phipps and Reeve (1967) have made reference to C. cf. beyeri from rocks of middle Ludlovian age in the Woolhope, and Malverns and Abberley areas. These specimens have not been seen by the present author but may represent C. lawsoni

C. lawsoni and C. puellaris are the last calymenids in the British succession.

Calymene aff. C. lawsoni Shirley, 1962

Plate 37, figs. 1-5.

MATERIAL. Two cranidia, LM 2859, DJS/145; one pygidium DJS/146. All the specimens were collected by Dr. J. Dalingwater, Univ. of Manchester.

OCCURRENCE. Middle Elton Beds, Ludlow Series, Upper Millichope, Wenlock Edge, Shropshire.

DISCUSSION. This species is very close to C. lawsoni. The material at hand shows the following differences from the Leintwardinian species: The posterior border furrow is shorter (exs.) and considerably less deeply impressed; the axial furrow (cranidium) is much narrower (tr.); the most anterior part of the fixed cheek descends steeply forwards; there is no linear arrangement of large tubercles on the median glabellar lobe or pygidial axis; the pygidial axis appears to narrow more sharply posteriorly.

In terms of cranidial morphology C. aff. lawsoni is a more likely ancestor of lawsoni than any other species. Shergold and Shirley (1968, p. 135) record a Calymene cf. blumenbachi from the Lower Elton Beds, upper Middle Elton Beds and Lower Bringewood Beds of Wenlock Edge which may represent the same species as figured here.

Calymene neointermedia R. &. E. Richter, 1954

Plate 37, figs. 6-11; Plate 38, figs. 1-10; Plate 39, figs. 1-4, 6, 7.

1885 Calymmene intermedia n.; Lindström, p. 71, pl. 15, figs. 8-12, non figs. 5-7.

? 1894 Calymmene intermedia Lindstr.; Schmidt, p. 16, pl. 2, figs. 2, 3, non fig. 1.

1901 Calymmene intermedia LDM.; Lindström, p. 48, pl. 3, figs. 6, 7.

non 1909 *Calymmene intermedia*; Moberg & Grönwall, pl. 3, figs. 15, 16.

non 1917 *Calymene intermedia*, Lindström; Reed *in* Gardiner, p. 168.

non 1920 *Calymene intermedia*; Gardiner, pp. 207, 218.

1921 *Calymmene intermedia* Lindstr.; Hede, pp. 61, 99 (*pars*),? pp. 58, 59, 60, *non* pp. 68, 69.

1933 *Calymene intermedia* Lindström, 1885; Shirley, pl. 1, fig. 16.

non 1937 *Calymene intermedia* Lindström; Straw, p. 452.

1954 *Calymene* (*Calymene*) *neointermedia* n.n.; R. & E. Richter, p. 19.

non 1955 *Calymene intermedia* Lindström; Lawson, p. 112.

non 1959 *Calymene neointermedia* (R. & E. Richter); Walmsley, p. 514.

non 1960 *Calymene neointermedia* (R. & E. Richter); Squirrell & Tucker, p. 177.

? 1960 *Calymene neointermedia* (R. & E. Richter); Regnell *in* Regnell & Hede, p. 30. *non* p. 31.

1960 *Calymene neointermedia* Rud. & E. Richter; Hede, *in* Regnell & Hede p. 82, *non* pp. 80, 81, 83.

non 1962 *Calymene neointermedia* R. & E. Richter; Whitaker, p. 160.

non 1963 *Calymene neointermedia* (R. & E. Richter); Holland, Lawson & Walmsley, pp. 117, 118, 126, 145, 147, pl. 6, figs. 4, 7.

1968 *Calymene neointermedia* R. & E. Richter; Haas, p. 98, text-figs. 16c, d.

? 1967 *Calymene neointermedia* R. & E. Richter; Phipps & Reeve, p. 367.

non 1968 *Calymene neointermedia*; Shirley & Shergold, p.135.

? 1970 *C. neointermedia*; Kaljo, p. 154.

1970 *C. pompeckji* KUMMEROW, 1928; Schrank, p. 120, pl. 1, fig. 4, ? fig. 6, *non* fig. 5, pl. 2, figs. 1-3, ? fig. 7.

non 1971 *Calymene neointermedia*; Cave & White, pp. 248, 252, 253.

non 1971 *Calymene neointermedia* R. & E. Richter; Shaw, p. 361.

HOLOTYPE. A damaged complete specimen which is partially enrolled; RM Ar6225; figured Lindström 1885, pl. 15, figs. 11, 12, also Shirley 1933, pl. 1, fig. 16, also Schrank 1970, pl. 1, fig. 4 and here Pl. 37, fig. 9.

TYPE STRATUM AND TYPE LOCALITY. Hemse Beds, Petesvik, parish of Hablingbo, Gotland.

Martinsson (1962, p. 54) lists an ostracode fauna of Craspedobolbina percurrens, C. robusta and Amphitoxotis curvata from Petes in the parish of Hablingbo; this fauna is characteristic of the older, south western part of the Hemse Beds. Hede (in Regnell and Hede 1960, p. 82, Loc. 44) records a conconcomitant graptolite fauna of Monograptus chimaera and M. nilssoni. The strata at the type locality is therefore of lower Ludlow age (see Martinsson 1967, p. 360).

ADDITIONAL MATERIAL. Ninety-five specimens, eighty of which are complete (though often damaged) individuals: RM Ar6218-220, RM Ar6228, RM Ar27079-083, RM Ar27104, RM Ar27141-149, RM Ar27153-154, RM Ar27157, RM Ar27159, RM Ar47788-794, RM Ar47796-798, RM Ar47800-803, RM Ar47840-844, RM Ar47856-857, BM 58676, BM 43690 (2 specimens), BM It 9145 (2 specimens), RSM 1967. 58. 117.

DIAGNOSIS. Cephalic outline bow-shaped. Preglabellar area long and moderately upturned. Outer part of posterior border furrow narrow, and in section like an open-V. Palpebral lobe moderately upturned. Width of cranidium in front of palpebral lobes about 1.9 times as wide as glabella at lobe 2p. Free cheek descends in evenly convex fashion from eye socle to lateral border furrow. Thorax has thirteen segments.

DESCRIPTION. Cephalon about twice as wide as long, in general shaped like a bow with anterior margin of cranidium sometimes projecting beyond general outline. Glabella subtrapezoidal to weakly bell-shaped in outline, about 1.2 times as long as wide and about equal in width to postocular part of fixed cheek. Occipital ring about equal to or slightly less than width of glabella, weakly convex in profile and falls gently to occipital furrow, in dorsal view narrows rather sharply behind basal lobes to axial furrow. Lateral lobe 1p just less than one third as wide as glabella, separated from median lobe by very shallow depression. Lateral furrow 1p deep, fairly narrow and almost transversely directed between lobes 1p and 2p, is directed more backwards on reaching central glabellar area. No intermediate lobe present. Elongate (tr.) or subcircular lateral lobe 2p is joined abaxially to genal buttress and confined adaxially by shallow furrow. Lateral furrow 2p transversely directed. Small lobe 3p runs down side of glabella into axial furrow. Weak 4p lobe very rarely present. Frontal lobe about 0.7 times as wide as glabella at lobe 1p,projects in front of fixed cheek, in dorsal view has well rounded anterolateral margins and a rather blunt to weakly arched anterior margin which falls steeply to, and is sharply undercut by, preglabellar furrow. In profile glabella reaches well above fixed cheek; dorsal surface is horizontal to lobe 3p.

Axial furrow very shallow outside occipital ring, becomes very much deeper beside lobes 1p and 3p. Anterior pit sited on inner side of axial furrow below side of frontal glabellar lobe. Preglabellar furrow is very wide. Preglabellar area is shovel-like, anterior side of preglabellar furrow slopes forwards and moderately upwards to the dorsal, uppermost edge of anterior border. The latter turns sharply over and passes into outer side of anterior border which runs downwards and very slightly backwards to rostral suture. In lateral profile dorsal surface of anterior border reaches as high as half way up anterior face of frontal lobe. Anterior margin is well rounded in dorsal view.

Posterior border widens gradually between axial furrow and fulcrum, expands more rapidly from fulcrum to facial suture due to backward flexure of posterior margin. Posterior border furrow relatively narrow (exs.) and in section is shaped like an open V, its anterior side is wider and less steeply sloping than the posterior, it pinches out abaxially well before facial suture. Highest point of fixed cheek is opposite lobe 2p, from here preocular part of cheek descends steeply forwards , and postocular part somewhat less steeply backwards to posterior border furrow. Palpebral lobe is large - at least as long (exs.) as lobe 1p, in frontal view it is continuous with the upward and outwardly directed slope of the fixed cheek, its outer margin is broadly arcuate or sometimes slightly pointed. Postocular part of fixed cheek is rather wide (tr.) and narrow (exs.). Posterior branch of facial suture directed transversely from eye lobe for a short distance before turning gently backwards to run onto lateral border where it swings backwards (and in some specimens slightly outwards) to bisect genal angle. Anterior branch of suture runs forwards and fractionally inwards to anterior margin; it turns sharply inwards across anterior face of border to meet rostral suture.

Void for visual surface of eye is large and reniform. Eye socle is rather broad and separated from main field of free cheek by marked break in slope and shallow furrow. Between shallow lateral border furrow and eye socle the cheek is steeply sloping and moderately convex (tr.). Lateral border furrow continues anteriorly in front of fixed cheek and runs into preglabellar furrow, posteriorly it fades on approaching facial suture. Dorsal side of lateral border rolls over and under into ventral side which is broadest at rostral plate and gradually narrows towards genal angle.

Rostral suture approximately parallels anterior margin; connective sutures are straight or very weakly abaxially convex, and quite strongly convergent; inner arc of border sector bends downwards and backwards more sharply near connective suture, its outline matches that of postaxial sector of pygidium - thus ensuring tight fit during enrollment. Border sector of rostral plate is about 2.7 times as wide (tr.) as long. Hypostome wider (tr.) than long. Anterior margin gently convex forwards. Narrow anterior border reflexed ventrally; anterior border furrow weak, only defined between anterior wings. Anterior lobe of median body bears a prominent ventrally directed projection which is sited on median line two-thirds of the distance from anterior margin to median furrow. Anterior part of anterior lobe is sagittally concave and transversely convex. Median furrow is well marked between lateral border and slightly swollen, oval-shaped maculae, considerably weaker between the maculae. Crescent shaped posterior lobe is moderately convex (sag. & tr.), confined by weak lateral and posterior border furrows. Posterior margin is bifid as posterior border is extended into two relatively short, flat spines. Lateral border much narrower (tr.) and more convex than posterior border.

Thorax contains thirteen segments. Axis is strongly arched (tr.), tapers very gradually posteriorly. Axial ring quite strongly convex sagittally, becomes less convex and wider (exs.) at shallow axial furrow but is not swollen. Articulating furrow deepest abaxially. Articulating half-ring rises sharply from articulating furrow, is moderately convex (sag.) and at least two thirds as long as axial ring. Pleurae rather long (tr.) and narrow. Posterior pleural band about twice as wide and higher than anterior pleural band, in profile quite strongly convex, narrows adaxially to form narrow, bounding rim to pleural facet. Pleural furrow sharply incised, deepest at fulcrum, shallows towards axial furrow and on pleural facet. Posterior outline of pleural facet more rounded in anterior than posterior pleurae.

Pygidium is small. Axis much less convex (tr.) than thoracic axis, contains six axial rings and a minute, posteriorly rounded terminal axial piece. At least first four axial rings are defined posteriorly by a complete ring furrow, all ring furrows are deepest near axial furrow. Pleural region slopes very steeply away from axial furrow, contains five pleural furrows which fade rapidly on reaching pygidial cincture, and five interpleural furrows which are very weak adaxially but become more distinct toward lateral margin. Fifth interpleural furrow forms side of postaxial sector which does not protrude posteriorly, but falls vertically from terminal axial piece.

Glabella, dorsal surface of anterior border and inner part of fixed cheek are covered with large (up to about 0.5 mm in diameter) widely spaced tubercles nearly all of which are perforate. There is a pairing of some of these larger tubercles on posterior part of median glabellar lobe: there is one tubercle either side the median line near the inner neck of lobe 1p, and one tubercle opposite (tr.) posterior margin of lobe 2p. Scattered in between the larger tubercles are a few smaller tubercles. All cephalic furrows smooth except for an occasional very fine pustule. Outer part of fixed cheek and free cheek between eye socle and lateral border furrow contain only a few very widely spaced small tubercles. Lateral border, outer side of anterior border and rostral plate covered with closely-spaced, flat-topped tubercles which are of medium-size and rounded on rostral plate but become smaller and a little more elongate towards genal angle. Axial ring of thorax has a row (tr.) of large, perforate tubercles (as on glabella) which continue onto dorsal surface of posterior pleural band. Otherwise thorax apparently largely devoid of ornament except for very fine pustules on pleural facets, and very small tubercles on most distal parts of posterior pleural bands. Innermost part of pygidial pleural region smooth, outer part of pleural region, postaxial sector and central part of axis covered with pustules and small to medium sized tubercles which are close together.

ONTOGENY. More than ninety specimens of C. neointermedia have been measured; the smallest specimen has a glabellar length of 3.1 mm and the largest specimen of 10.8 mm.

Holaspid period. Eighty-one complete individuals are at hand and all of these have thirteen thoracic segments. Included within these eighty one specimens are the two smallest individuals measured - which have glabellar lengths of 3.1 mm (RM Ar47789) and 3.2 mm (RM Ar47842). There are no meraspides present in the sample.

Vision. The smallest specimen with the free cheek in place and the palpebral lobe intact (RM Ar47842 - glabellar length of 3.2 mm) already shows a wide, reniform void which accommodated the visual surface of the eye (cf. C. tuberculosa).

Contact of 2p lobe and genal buttress. All of the specimens examined have the 2p lobe in contact with a genal buttress.

Genal spines. None of the specimens show a distinct genal spine though, as in C. tuberculosa, some of the smaller cranidia (with a glabella shorter than about 4.5 mm) have the posterior margin flexed very slightly backwards near the facial suture which indicates the spine has not long disappeared.

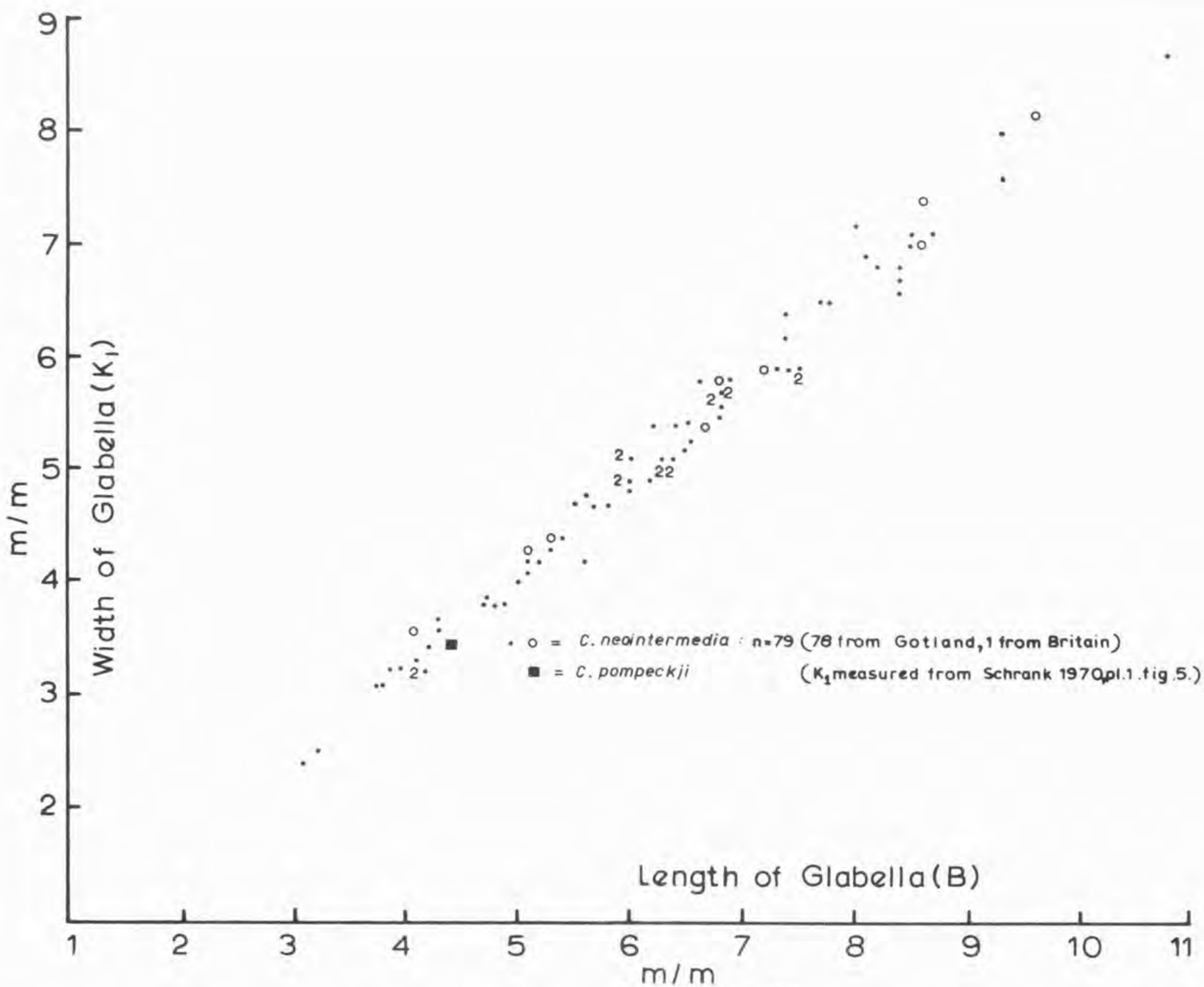
Growth of glabella and preglabellar area. A plot of glabellar length (variate B) against glabellar width (K_1) suggests a rectilinear relationship exists between these two variates during the holaspid period of growth. In contrast, the preglabellar area (variate D) appears to become relatively longer in comparison with the length of the glabella during ontogeny. In specimens with a glabellar length of about 4.0 mm the preglabellar area is about a quarter as long, in specimens with a glabellar length of about 8.5 mm the preglabellar area is about a third as long.

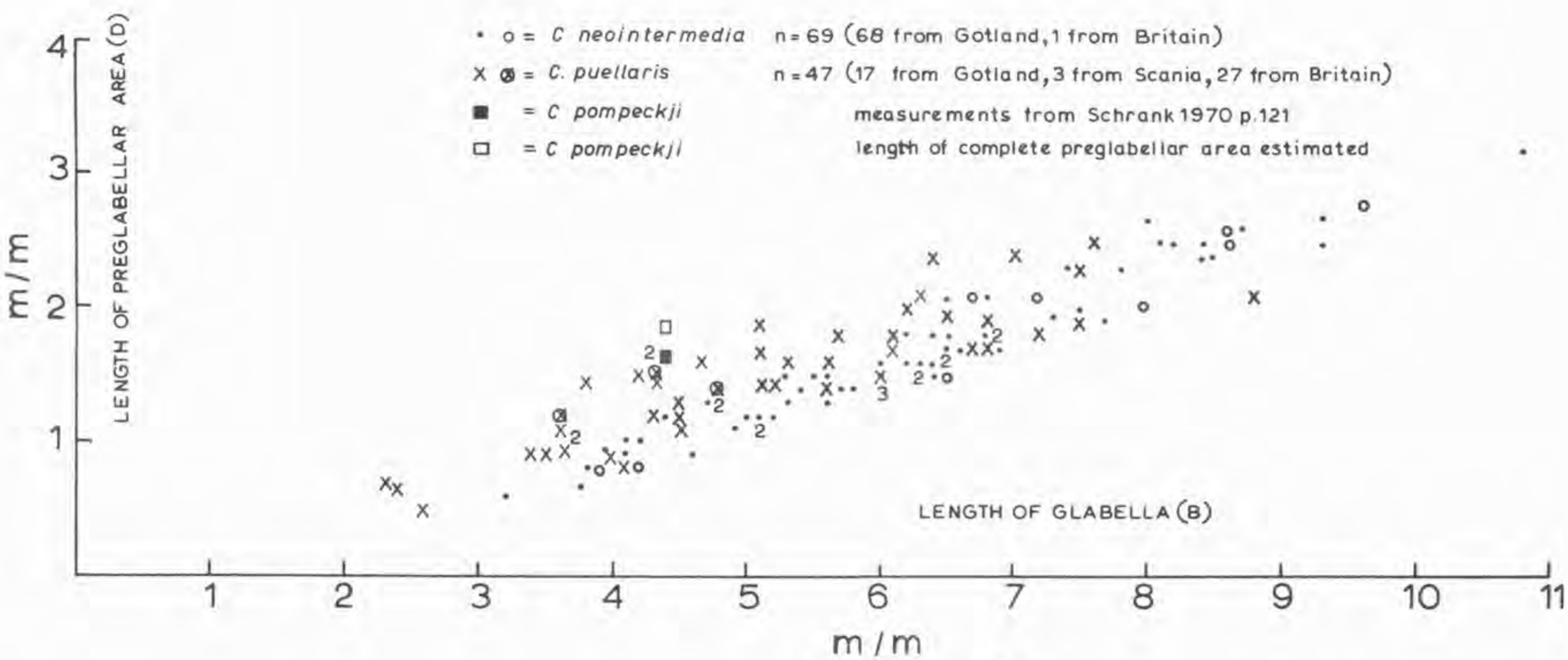
DISCUSSION. The synonymy list indicates the extent to which C. neointermedia has been referred to by palaeontologists and biostratigraphers during the last ninety years. But with the exception of Schrank (1970) there has been no full revision of the species, and during the last seventy years only two authors (Shirley 1933, pl. 1, fig. 16; Schrank 1970, pl. 1, fig. 4, pl. 2, figs. 1-3) have figured material from Gotland. The conclusions from this study are based on an examination of more than ninety specimens, about half of which are known to have come from the type locality.

R. & E. Richter (1954, p. 19) recognised that C. intermedia Lindström, 1885 was a junior primary homonym (of C. intermedia Münster, 1840 = Encrinurus variolaris (Münster)) for which they erected the new name of neointermedia. At the same time the Richters designated one of Lindström's figured specimens as the type. In his revision Schrank contended that C. neointermedia R.& E. Richter was a junior synonym of Calymene pompeckji Kummerow, 1928, the latter species being founded on one small specimen from a glacial erratic. Kummerow (1928, p.9) believed this erratic to have been derived from the Beyrichienkalk,though Schrank considered a middle Ludlow horizon within the Graptolithengestein to be more likely.

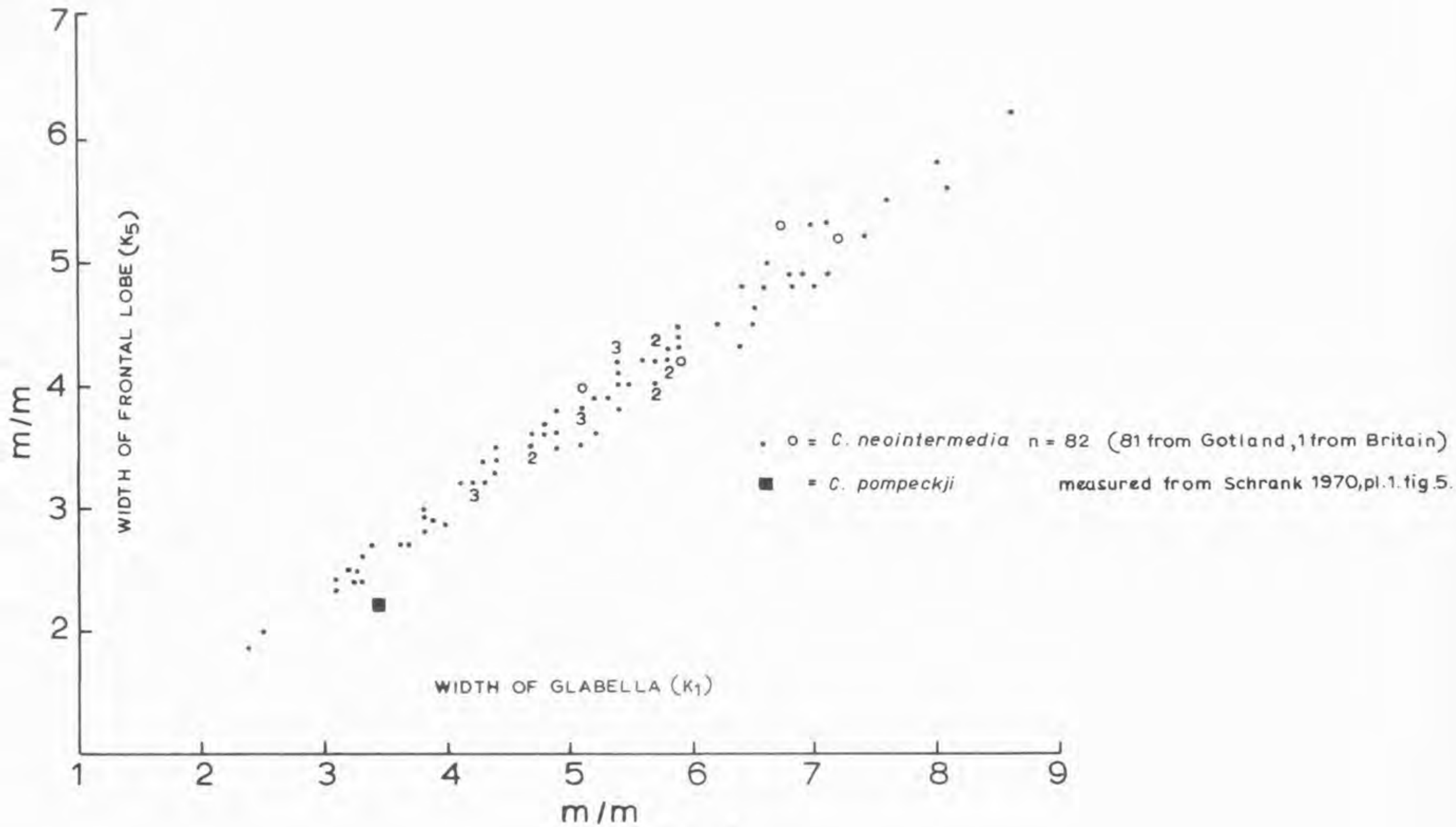
C. pompeckji is in some respects similar to C. neointermedia, in particular both have a long, scoop-like preglabellar area, but there are at least five differences which lead me to regard them as separate species, and they may belong to separate genera.

1) The holotype of pompeckji has a glabella which is 4.4 mm long yet has no papillate-buttress structure at lobe 2p. Schrank accounted for the absence of this feature by the fact that the holotype was a juvenile individual (see ontogeny of C. tuberculosa herein). However all of the neointermedia specimens I have seen from Gotland have this structure fully developed, and this includes thirteen specimens with a glabella


9
8
7
6
5
4
3
2
m/m
Width of Glabella (K_1)
• o = C. neointermedia : n=79 (78 from Gotland, 1 from Britain)
■ = C. pompeckji
(K_1 measured from Schrank 1970, pl. 1, fig. 5.)
Length of Glabella (B)
1
2
3
4
5
6
7
8
9
10
11
m/m
TEXT-fig. 2

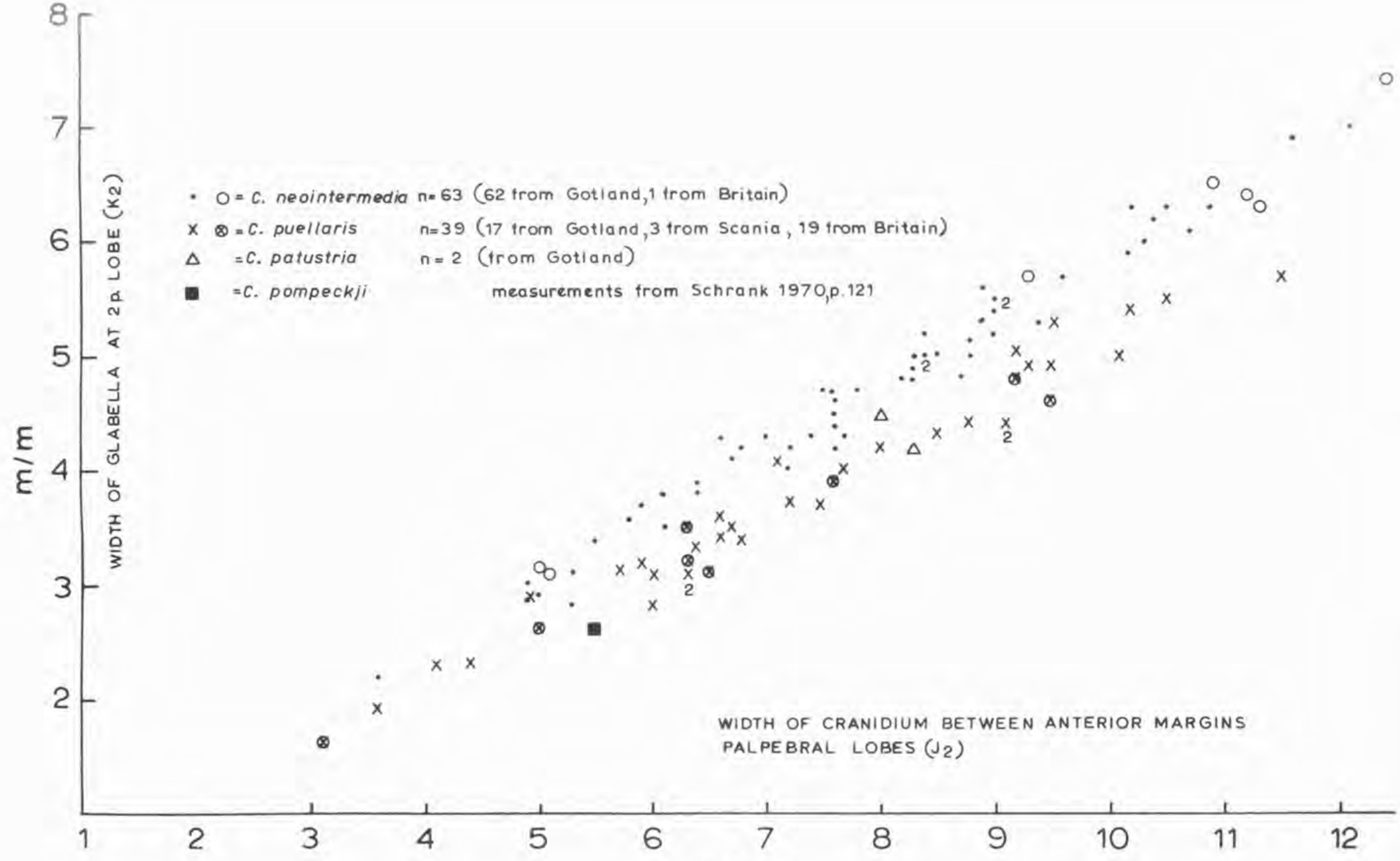

• o = C neointermedia n = 69 (68 from Gotland, 1 from Britain)
X ⊗ = C. puellaris n = 47 (17 from Gotland, 3 from Scania, 27 from Britain)
■ = C pompeckji measurements from Schrank 1970 p.121
□ = C pompeckji length of complete preglabellar area estimated
LENGTH OF PREGLABELLAR AREA (D)
m/m
LENGTH OF GLABELLA (B)
m/m
1
2
3
4
5
6
7
8
9
10
11

TEXT-fig. 3



7
6
5
4
3
2
m/m
WIDTH OF FRONTAL LOBE (K5)
WIDTH OF GLABELLA (K1)
1
2
3
4
5
6
7
8
9
m/m
• o = C. neointermedia n = 82 (81 from Gotland, 1 from Britain)
■ = C. pompeckji measured from Schrank 1970, pl. 1. fig. 5.

TEXT - fig. 4


• ○ = C. neointermedia n=63 (62 from Gotland, 1 from Britain)
x ⊗ = C. puellaris n=39 (17 from Gotland, 3 from Scania, 19 from Britain)
△ = C. patustria n = 2 (from Gotland)
■ = C. pompeckji measurements from Schrank 1970, p. 121
WIDTH OF GLABELLA AT 2p LOBE (K2)
m/m
WIDTH OF CRANIDIUM BETWEEN ANTERIOR MARGINS PALPEBRAL LOBES (J2)
m/m

TEXT-fig. 5

shorter than 4.4 mm (see text-fig. 2), the smallest (RM Ar47789) being 3.1 mm long. Measurements taken on C. tuberculosa and C. puellaris indicate that the genal buttress and 2p lobe meet in these species when the glabella is between 2.8 mm to 3.0 mm long, and 2.4 to 2.8 mm long,respectively. In C. lawsoni the lobe and buttress meet when the glabella is somewhere between 2.0 and 2.9 mm long. Unless the development of this structure is in a state of arrest in pompeckji, it is unlikely that it is synonymous with neointermedia. Moreover unless pompeckji is a species which develops the structure comparatively late in ontogeny, its assignment to Calymene is seriously challenged.

2) The anterior tip of the preglabellar area is missing in pompeckji, but both the actual and estimated measurements of its length are substantially greater than those of neointermedia specimens of equivalent size (see text-fig. 3).

3) The anterior margin of the cranidium in pompeckji seems to be converging medially in a U or V-shape rather the more rounded outline of neointermedia.

4) Compared with neointermedia (especially small specimens) the outline of the glabella in pompeckji is much more strongly bell-shaped, the frontal lobe being narrower relative to the glabellar width at 1p lobes (see text-fig. 4).

5) The anterior branches of the facial suture in pompeckji are wider apart relative to the width of the glabella at lobe 2p (text-fig. 5).

The second and the last of these distinctions place C. pompeckji closer to C. puellaris but these two species clearly differ in the number of thoracic segments (Kummerow recorded thirteen in pompeckji; puellaris has twelve), and the development of the papillate-buttress structure. The present evidence suggests pompeckji is allied with the three non-buttressed species from the Polish Ludlovian which Tomczykowa (1970) assigned to Spathacalymene Tillman, 1960. These taxa will be discussed more fully elsewhere.

C. neointermedia is most closely related to C. puellaris and C. patustria sp. nov; and an account of the differences between these species is given below. The pairing of the glabellar tubercles in neointermedia is far less distinct and less continuous anteriorly than in C. lawsoni Shirley, 1962 but it suggests some degree of relationship between the two species. An interesting feature of neointermedia and puellaris is the palpebral lobe, which even in large holaspides is rather long (exs.) - often having a greater length than lateral lobe 1p. In complete contrast is the very small palpebral lobe of C. frontosa.

OCCURRENCE. C. neointermedia has for many years been regarded as an index fossil for strata of Upper Leintwardine age in Britain, yet the type stratum on Gotland is lower Ludlow in age. All the specimens I have examined from the British Leintwardinian can be assigned to C. puellaris and not C. neointermedia (see discussion of puellaris below). Of the ninety five specimens here referred to neointermedia, all except two are from Gotland. About half the Gotland specimens are known to have come from the type locality of Petesvik; all the other specimens except one are more generally labelled - such as "Silurian, Gotland" or "Hablingbo (? parish of), Gotland" - though preservational and lithological criteria strongly suggest they also come from the Hemse Beds at or in the vicinity of Petesvik. The one specimen (RM Ar27104) here referred to neointermedia which is specifically labelled as not coming from Petesvik, is from the Hemse Beds at Havdhem. The parish of Havdhem contains strata belonging to both the Hemse and Eke Beds. This specimens is in a box together with three specimens of C. puellaris but the differing preservation of both species suggests they came from separate localities or horizons.

In the British Museum there are two specimens (both on the same slab - BM It9145) which can with certainty be assigned to neointermedia; they are given as coming from the Wenlock Limestone of the Malverns and there is little reason to doubt the label information. The occurrence of neointermedia at this horizon in Britain was somewhat disturbing until the distinction between neointermedia and puellaris became evident. The Malverns specimens are only slightly older than specimens from the type locality. In the Royal Scottish Museum, Edinburgh there is a specimen (RSM 1967. 58. 117) of C. neointermedia which is labelled as coming from Dudley, but the curatorial history of this specimen leaves much to be desired and in all respects it is a typical Gotland example.

Regnell (in Regnell & Hede 1960, pp. 30, 31) lists neointermedia from the Colonus Beds (= lower Ludlow) and division 1 of the Öved-Ramsasa Beds of Scania (? = upper part of Hemse Beds on Gotland; see Martinsson 1967, pp. 371, 372, text-fig. 3). I have not examined material from the former horizon but specimens from Klinta (RM Ar32767, RM Ar32773, RM Ar32778), which I assume to be from the latter horizon (see Regnell 1960, p. 30), can be attributed to C. puellaris.

Schrank (1970, pl. 2, fig. 1) has figured material of neointermedia from glacial erratics of the Graptolithengestein.

Schmidt (1894, p. 16, pl. 2, figs. 1-3) recorded the species from Zone K of the Baltic upper Silurian and Kaljo (1970, p. 154) from the Kaugatuma Beds (= Downtonian in age; Cocks et al. 1971, fig. 9) of Estonia. Schmidt's material needs revision, Kaljo's material to be formally described.

In summary, the present author has recorded neointermedia from the Hemse Beds (possibly restricted to the lower part) on Gotland and the Wenlock Limestone of the Malverns.

Calymene puellaris Reed, 1920
Plate 39, fig. 5; Plate 40, figs. 1-7;
Plate 41, figs. 1-9; Plate 42, figs. 2, 5.

1848 Calymene tuberculosa, Salter; Salter (pars) p. 342.

1849 Calymene tuberculosa; Salter (pars), p. 8, pl. 8, figs. 8, 8* (GSM 19690), non pl. 8, figs. 1-7.

1851 Calymene tuberculosa (Salt); McCoy (pars) in Sedgwick & McCoy, p. 167.

1873 Calymene tuberculosa, Salter; Salter, p. 166.

1917 Calymene intermedia Lindström; Reed in Gardiner, p. 168.

1920 Calymene intermedia;Gardiner, pp. 207, 218.

1920 Calymene papillata, var. nov. puellaris; Reed in Gardiner, pp. 207, 218, 221, unnumbered text-fig. on bottom left side of p. 221 (holotype - SM A3320).

1933 Calymene papillata var. puellaris REED, 1921; Shirley, p. 63, pl. 1, fig. 15 (holotype of C. puellaris).

1937 Calymene intermedia Lindström; Straw, p. 452.

1955 Calymene intermedia Lindström; Lawson, p. 112.

1959 Calymene neointermedia (R. & E. Richter); Walmsley, p. 514.

1960 Calymene neointermedia (R. & E. Richter); Squirrell & Tucker, p. 177.

1960 Calymene neointermedia (R. & E. Richter); Regnell in Regnell & Hede, p. 31.

1960 Calymene neointermedia Rud. & E. Richter; Hede in Regnell & Hede, pp. 80, 81, 83, non p. 82.

1962 Calymene neointermedia R. & E. Richter; Whitaker, p. 160.

1963 Calymene neointermedia (R. & E. Richter; Holland, Lawson & Walmsley, pp. 117, 118, 126, 145, 147, pl. 6, figs. 4, 7.

? 1967 Calymene neointermedia R. &. E. Richter; Phipps & Reeve, p. 367.

1968 Calymene neointermedia; Shirley & Shergold, p. 135.

1971 Calymene neointermedia; Cave & White, pp. 248, 252, 253.

1971 Calymene neointermedia R. & E. Richter; Shaw, p. 361.

HOLOTYPE. A damaged internal mould of a complete specimen; SM A3320; figured Reed in Gardiner 1920, unnumbered text-fig. on bottom left hand side of p. 221, also Shirley 1933, pl. 1, fig. 15, and here Pl. 42, figs. 2, 5.

TYPE STRATUM AND TYPE LOCALITY. Middle Ludlovian, quarry one third of a mile ENE of Longhope Church, May Hill, Gloucestershire, (= Locality M24 of Gardiner 1920).

It is probable the holotype came from the Lower Longhope Beds (= Upper Leintwardinian in age).

ADDITIONAL MATERIAL. More than seventy specimens, sixteen of which are complete. The following specimens are from Gotland: RM Ar27076-078, RM Ar27103, RM Ar27105-27124, RM Ar27126-128, RM Ar27137, RM Ar27139, RM Ar47785-787, RM Ar47795.

The following specimens are from Scania: RM Ar32767, RM AR32778, RM Ar32773.

The British material comprises the author's own collections, together with specimens from the Sedgwick Museum, Geological Survey, Birmingham University (J. Lawson Coll.), British Museum, and from Mr. R. Marsh (Norwood Technical College).

DIAGNOSIS. Preglabellar area long and fairly strongly upturned. Outer part of posterior border furrow is wide and flat bottomed. Palpebral lobe about horizontal. Width of cranidium in front of palpebral lobes about 1.9 times as wide as glabella at lobe 2p. Free cheek between eye socle and lateral border furrow is angular in section (tr.). Thorax has twelve segments.

DESCRIPTION. C. puellaris is similar to C. neointermedia which has been described in full. The two species are compared below.

ONTOGENY.

Holaspid period. Seventeen of the specimens examined (including the holotype) are complete, though often damaged. All of these have only twelve thoracic segments - which must therefore be regarded as the normal complement for holaspides of the species. The observed range for the glabellar length (variate B) in the complete specimens is from 4.2 mm (RM Ar27114) to 7.6 mm (RM Ar27126).

The following specimens with twelve segments come from Gotland: RM Ar27076-077, RM Ar27103, RM Ar27105-106, RM Ar27114, RM Ar27126-128, RM Ar27137, RM Ar47787. Most of these are well preserved and have the cuticle remaining.

The following specimens with twelve segments are from Britain: SM A3320 (holotype), BM It577 - from the Ludlow Anticline, GSM 19688-690 - from the Usk Inlier, GSM TMcKH 64 - from the Lake District. This material is not as well preserved as the Gotland examples, and all the specimens are internal moulds. GSM 19688-690 are originals of Salter (1849 - see synonymy).

Contact of 2p lobe and genal buttress. All specimens with the cuticle remaining and all casts of external moulds show the second glabellar lobe in contact with a genal buttress. The smallest specimen amongst this material has a glabella 2.8 mm long (RM Ar27115).

The internal moulds in the sample do not, naturally, have the axial furrow fully bridged though all of them show a papillate 2p lobe and the remains of a genal buttress. This includes the following three specimens which have a glabella shorter than 2.8 mm: DJS/136 (2.3 mm), BM unnumbered (2.4 mm) and DJS/54 (2.6 mm). It is impossible to determine whether the papillate - buttress structure in each of these cranidia was fully developed or not, though in at least one of them (BM unnumbered) the genal buttress appears to be only incipient.

In puellaris the 2p lobe seems to make contact with the genal buttress when the glabella is between about 2.4 and 2.8 mm long, though extra specimens are needed for a more precise determination. From the present material it is not possible to say whether the specimens with a glabellar length within this range are holaspides or meraspides.

Genal spine. A few British puellaris specimens show a distinct genal spine. This feature is not unexpected in very small specimens (for example BM unnumbered - glabella 2.4 mm long), but two cranidia (BM It 576b; M1) with glabellae 3.7 mm and 4.4 mm (estimated) long still retain a spine on the fixed cheek. It is unknown to what extent this applies to other specimens within this size - range, but it seems unlikely that individuals with a glabella in the region of 4.0 mm long can be anything other than holaspides. It is a characteristic of puellaris cranidia that the posterior margin does not swing markedly forwards near the genal angle as in adults of most Calymene species. Instead the distal corner of the fixed cheek is often drawn backwards - which supports the idea that C. puellaris loses its genal spine comparatively late in ontogeny.

The smaller of the above two cranidia (BM It 576b) has the 2p lobe firmly joined to a genal buttress; the larger one is a steinkern.

DISCUSSION. C. puellaris was erected on the basis of one specimen. Reed believed that puellaris was closely related to Lindtröm's species from the middle Ludlow of Gotland, C. papillata (= Papillicalymene papillata). Shirley (1933, p. 63) refuted this claim and suggested puellaris "should be placed with or near to C. intermedia" Lindström (= C. neointermedia R. & E. Richter), but thought there was "no justification for raising a new species or variety".

Though the holotype of puellaris is an internal mould and badly damaged, it is complete and sufficient remains of the thorax, preglabellar area and fixed cheek to identify the species. Reed (1920, p. 207) also recorded C. intermedia from the type locality of puellaris; these specimens (SM A36814-815) are extant, well preserved, and regarded here as conspecific with puellaris. Good material of puellaris is also available from Gotland.

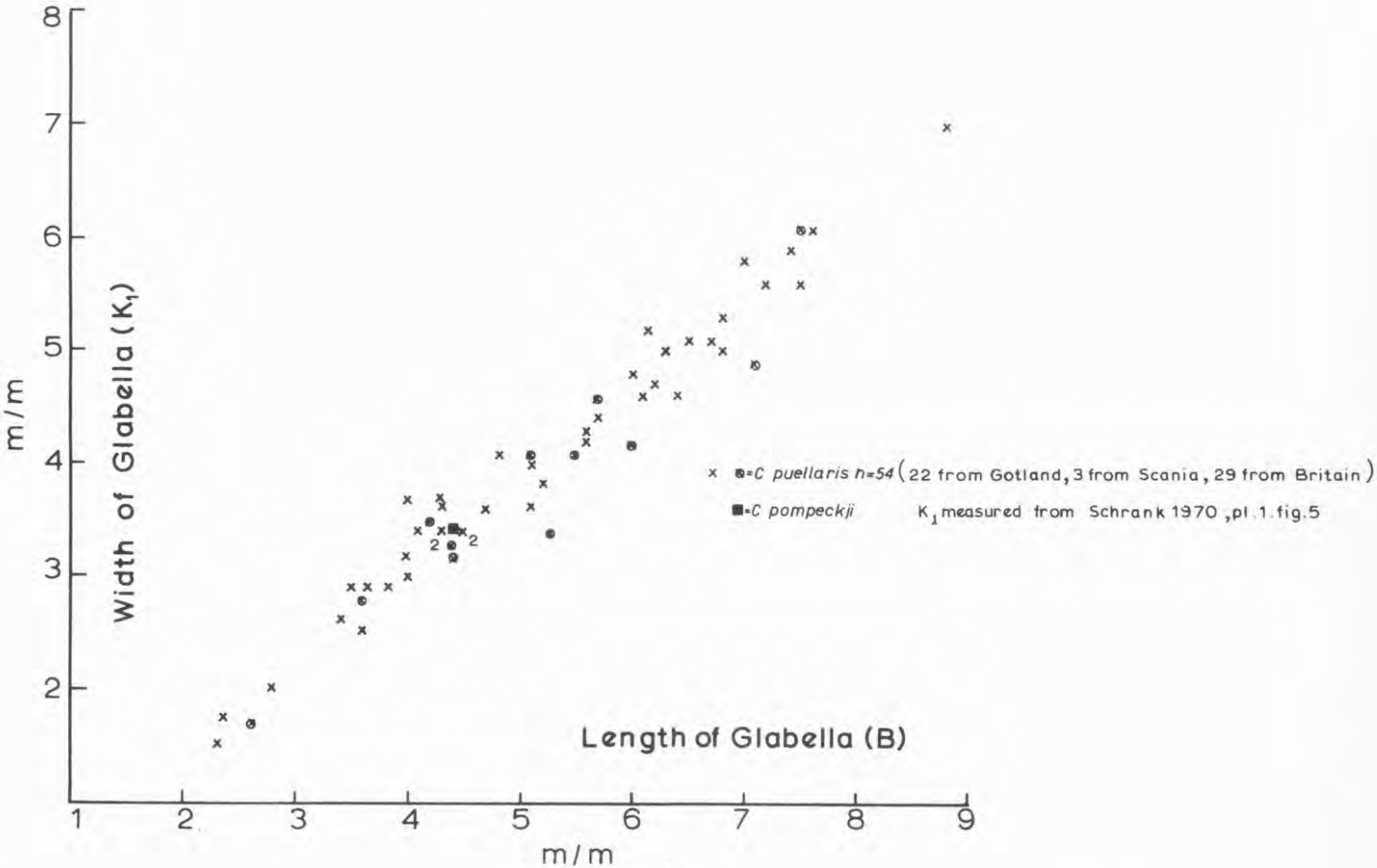
It is particularly unfortunate that Reed's species has not been rehabilitated prior to the present study. There is no doubt that what many authors have recorded as C. neointermedia in rocks of Leintwardinian age throughout the Welsh Borderlands and elsewhere is in fact C. puellaris. The two species are indeed similar, and neointermedia almost certainly gave rise to puellaris, but they can be consistently separated on the basis of several cranidial and thoracic characters. These are:

1) Number of thoracic segments. C. neointermedia has thirteen. It was Reed's opinion that the holotype of puellaris had only twelve, though Shirley (1933, p. 63) said thirteen. I can find only twelve, and this number is confirmed by other Welsh Borderland and Gotland specimens of puellaris (see ontogeny and compare RM Ar27126 with BM It9145).

2) The posterior border furrow of puellaris is very much wider (exs.), and more trench-like than that of neointermedia, especially abaxially from the fulcrum where the furrow is as wide as or wider than the dorsal surface of the fixed cheek. The sides of this furrow in puellaris are steeper, and the base more flattened (compare RM Ar32767 with RM Ar47797 or RM Ar27126 with BM 43690).

3) In puellaris the posterior margin of the fixed cheek swings more backwards near the facial suture, the distal corner of the fixed cheek is drawn more posteriorly, and the genal spine is probably lost relatively later in ontogeny (see ontogeny).

4) In puellaris the main part of the free cheek between the eye socle and lateral border furrow is considerably more angular in section (tr.). This angularity is often continued onto the anterior part of the fixed cheek at the facial suture. In neointermedia the free cheek descends in an evenly convex fashion from the eye socle to lateral border furrow.


m/m
Width of Glabella (K_1)
8
7
6
5
4
3
2
1
2
3
4
5
6
7
8
9
m/m
Length of Glabella (B)
x ⊗=*C puellaris n=54* (22 from Gotland, 3 from Scania, 29 from Britain)
■=*C pompeckji* K_1 measured from Schrank 1970, pl. 1. fig. 5

Text-fig 6

5) The anterior branches of the facial suture in puellaris are wider apart relative to the width of the glabella at lobe 2p. (see text-fig. 5).

6) The preglabellar area in puellaris is more strongly upturned.

7) The palpebral lobe of puellaris is more horizontally inclined. Many puellaris cranidia have a relatively longer preglabellar area than those of neointermedia (text-fig. 3) but this does not seem to be a constant distinction between the two species. Also, the length of the preglabellar area and the glabellar length appear to be more highly correlated during ontogeny in neointermedia than in puellaris, but this may simply reflect the better preservational and geographical homogeneity of the neointermedia sample. The same applies to a plot of glabellar width against glabellar length in the two species (text-figs. 2,6).

Salter (1849) was the first to figure a specimen of puellaris (GSM 19690) - from the Ludlovian of the Usk Inlier. Because of its long, scooped preglabellar area he assigned it to Calymene tuberculosa Salter, 1848 non Dalman 1827 (= C. nodulosa Shirley, 1933). C. puellaris and C. neointermedia are not considered by the present author to be allied to nodulosa; the similarity in their preglabellar areas is thought to be the result of parallelism.

Although both species have only twelve thoracic segments, C. puellaris is quite distinct from C. frontosa Lindström, 1885 from the Upper Llandovery of Gotland. The two species are not closely related.

OCCURRENCE. C. puellaris is widely distributed - occurring throughout the Welsh Borderland, the Lake District, Gotland and Scania in rocks of middle Ludlow age.

1) Welsh Borderland and the Lake District:

a) Usk Inlier. Walmsley (1959) recorded neointermedia from the Lower Llangibby Beds (= Upper Leintwardinian). Specimens collected from this horizon by the present author and some in the Geological Survey are all referable to *puellaris*.

b) Builth. Straw (1937) records *intermedia* from the *Chonetoidea grayi* Beds (= Upper Leintwardinian). The only *Calymene* specimen (MI) examined from rocks of Upper Leintwardine age in this area is referable to *puellaris*.

c) May Hill. Lawson (1955) recorded *intermedia* from the Upper Blaisdon Beds, Lower and Upper Longhope Beds. Material examined (J. Lawson Colln. Birmingham University) from the Lower Longhope Beds (= Upper Leintwardinian) can be assigned to *puellaris*. It is probable this is the type stratum.

d) Woolhope. Squirrell and Tucker (1960) list *neointermedia* from the Lower and Upper Bodenham Beds. One specimen of *puellaris* has been collected from the Upper Bodenham Beds (= Upper Leintwardinian).

e) Malverns and Abberleys. The Wenlock Limestone of the Malverns has yielded two specimens of *C. neointermedia* (BM It9145; see previous discussion). I have not examined any Ludlovian calymenids from this area but Phipps & Reeve (1967)record *C. neointermedia* from the Mocktree Shale Member, Woodbury Shale Member, and Whitcliffe Flags Member .

f) Ludlow Anticline and Leintwardine. Holland, Lawson and Walmsley (1963) and Whitaker (1962) record *C. neointermedia* from the Upper Leintwardine Beds, and Whitaker (1962) from his Higher Lower Leintwardine Beds. Specimens of *puellaris* have been collected from the Upper Leintwardine Beds in both areas.

g) Wenlock Edge. Shergold and Shirley (1968, p. 135) list *C. neointermedia* from their High Upper Leintwardine Beds and Basal Upper Leintwardine Beds, and (Plate 15) from their Basal Upper Leintwardine Beds. I have examined material of *puellaris* from the High Upper Leintwardine Beds.

2) Gotland.

a) From the Hemse Beds at: Alva Kanal; Vanges Kanal; Burs; Burs Kanal; Rone Kanal vid Vesterlaus; Visne myr, Fardhem; ? Petesvik.

All of these localities except the last two are in the S and S E parts of the Hemse Beds which have yielded an ostracode fauna of Neobeyrichia lauensis N. scissa and Sleia equestris. (Martinsson 1967, p. 354). This fauna characterizes the youngest part of the Hemse Beds and is correlated (Martinsson 1967, p. 360) with the British Leintwardinian.

The parish of Fardhem is situated in the N central part of the Hemse Beds. This seems to lie in the Hammariella pulchrivelata - Neobeyrichia nutans zone of Martinsson (1967) which he correlated with the upper Bringewoodian. However some localities in the area N and N W of Hemse - which encompasses a part of the parish of Fardhem - have yielded an ostracode fauna with elements from younger beds, including N. lauensis. (see Martinsson, 1962, p. 54). The puellaris specimens from Fardhem may therefore be younger in age than Upper Bringewoodian.

Four specimens (RM Ar47785 - 787, RM Ar47795) referable to puellaris are labelled as coming from Petesvik (= lower part of Hemse Beds).

Three specimens (RM Ar27103, RM Ar27105 - 106) come from Havdhem. Both the Hemse and Eke Beds are present in this parish.

b) From the Eke Beds at: Lau backar (RM Ar27137) and Eke, Alvskogs (RM Ar27126). The Eke Beds are correlated with the Upper Leintwardinian and Lower Whitcliffian (Martinsson 1967, p. 360).

3) Scania.

Three specimens from Klinta (RM Ar32767, RM Ar32773, RM Ar32778) which have no horizon information but may come from division 1 of the Öved - Ramsasa Beds (see Regnell 1960, pp. 30, 31 and occurrence of C. neointermedia).

Calymene patustria sp. nov.

Plate 42, figs. 1, 3, 4, 6, 7; Plate 43, figs. 1-8.

1885 Calymmene intermedia n.; Lindström, p. 71, pl. 15, figs. 5-7.

DERIVATION OF THE NAME. From the Latin, patulus, spread-out, and stria, furrow, referring to the form of the lateral border furrow of the free cheek.

HOLOTYPE. An almost complete specimen which is enrolled; RM Ar47855; Pl. 42, figs. 1, 3, 4, 6, 7.

TYPE STRATUM AND TYPE LOCALITY. Lower part of the Hemse Beds (= lower Ludlovian), Petesvik, parish of Hablingbo, Gotland.

ADDITIONAL MATERIAL. Five complete, but damaged specimens, RM Ar6222 (figured Lindström 1885, pl. 15, fig. 5), RM Ar27150-151, RM Ar47858, RM Ar47797; one incomplete cephalon with the remains of several thoracic segments, RM Ar27152; one incomplete cranidium, RM Ar6221 (figured Lindström 1885, pl. 15, figs. 6, 7).

DIAGNOSIS. Cephalic outline subrectangular. Preglabellar area almost vertically upturned. Preglabellar furrow very deep. Adaxial part of fixed cheek quite strongly vaulted (exs.); anterior part of fixed cheek slightly overhanging. Palpebral lobe horizontal. Lateral border furrow and ventral side of lateral border exceedingly wide. Thorax has thirteen segments.

DISCUSSION. C. patustria is most closely related to C. neointermedia. The latter species has been described at length above and comment here will be confined to a comparison of the two taxa. Lindström (1885) noted a variety of C. neointermedia (= C. intermedia Lindström, 1885) which differed from the typical form in the nature of its preglabellar area and free cheek. Two of Lindström's originals (RM Ar6221-222) of this variety are extant and six other specimens have been found in the Riksmuseet Collections. These specimens represent a very interesting and, in some characters quite unique species of Calymene which is here formally distinguished from neointermedia. The new species differs from neointermedia in the following respects:

1) The shape of the cephalon is substantially more rectangular.

2) The occipital ring falls more steeply into the occipital furrow.

3) The preglabellar furrow is very much deeper, its anterior slope rising almost vertically before passing into the dorsal surface of the anterior border which nearly reaches above the frontal glabellar lobe (see lateral and frontal views).

4) In dorsal view the anterior margin of the cranidium is almost straight (tr.) or at most very weakly convex forwards; it does not project beyond the general cephalic outline.

5) The fixed cheek slopes (exs.) more steeply from the palpebral lobe to the posterior border furrow, and very much more steeply along the anterior branch of the facial suture to slightly overhang the adaxial continuation of the lateral border furrow. Thus in lateral view the profile of the fixed cheek is more strongly vaulted.

6) In frontal view the palpebral lobe is horizontally disposed; it does not continue the outward and moderately upward slope of the inner part of the fixed cheek as in neointermedia.

7) The free cheek between the eye socle and the lateral border is more steeply inclined and relatively narrower. The lateral border furrow is extraordinarily wide and anteriorly is gutter-like - the lateral margin becoming progressively more upturned towards the facial suture. In dorsal view there is no clear division or break in slope between the lateral border furrow and lateral border. The outer part of the border does not roll smoothly over and under (as in neointermedia) but is a very narrow edge which turns sharply through 180 degrees to

pass into the ventral side of the border.

8) The ventral side of the lateral border is considerably wider (tr.) and the border sector of the rostral plate very much longer (sag.).

The remarkable form of the free cheek in _C_. _patustria_ is unlike that of any other member of the family and immediately distinguishes the species. Its occurrence at Petesvik and its unquestionable likeness to _C_. _neointermedia_ suggest the possibility of a most unusual type of dimorphism. There is no size difference between those specimens assigned to _patustria_ and those of _neointermedia_, and no morphologically intermediate forms have been found between the two species. In the available samples of the two species, _C_. _neointermedia_ is in the majority by about twelve to one.

The form of the posterior border furrow in _patustria_ is like that of _neointermedia_, not _puellaris_, though the inclination of the palpebral lobe is the same as in _puellaris_. These three species form a compact group in deposits of latest Wenlock to middle Ludlovian age in Britain, Gotland and Scania.

OCCURRENCE. Only known from the lower Hemse Beds (= lower Ludlovian), Parish of Hablingbo, Gotland.

PROBOSCIDEAN TRENDS IN CALYMENID TRILOBITES FROM THE ORDOVICIAN AND SILURIAN OF N W EUROPE, THE UNITED STATES AND S E ASIA.

In a number of trilobite genera the cranidium or some part thereof exhibits a long, though often variably developed, anterior projection. This will be referred to here by the general name of a proboscis. Thus in the Calmoniidae Delo, 1935 this feature is manifested by Schizostylus Delo, 1935, Probolops Delo, 1935 and Paracalmonia Struve, 1958; in the Raphiophoridae Angelin, 1854 by Raphiophorus Angelin, 1854, Ampyx Dalman, 1827 and Lonchodomas Angelin, 1854. The Calymenidae are perhaps one of the more conservative trilobite groups, yet within this family at least seven phyletic lines exhibit a similar trend. In each lineage the most conspicuous development of this trend is shown by the following species:

1) Calymene nodulosa Shirley, 1933 from the Wenlock Shale, Cyrtograptus lundgreni Zone, of the Welsh Borderlands. This is here referred to a new genus.

2) Spathacalymene nasuta (Ulrich, 1879) from the Osgood Formation, Osgood, Ripley County, Indiana, U.S.A. In their correlation chart of North American Silurian rocks, Berry & Boucot (1970) regard the Osgood Formation of southern Indiana as being of Upper Llandovery (C_5-C_6 zones) age.

3) Spathacalymene flexuosa Tomczykowa, 1970 from the zones of Cucullograptus aversus and Saetograptus leintwardinensis, Upper Mielnik Beds (Ludlovian), Mielnik and Terespol boreholes, Poland. This is here referred to another new genus.

4) Thelecalymene mammillata (Hall, 1861) from the Elgin Shaly Limestone Member, Maquoketa Shale, Iowa, U.S.A. Whittington (1971, p. 132) regarded the Elgin Member as being of Upper Ordovician Richmond, or possibly slightly older, age.

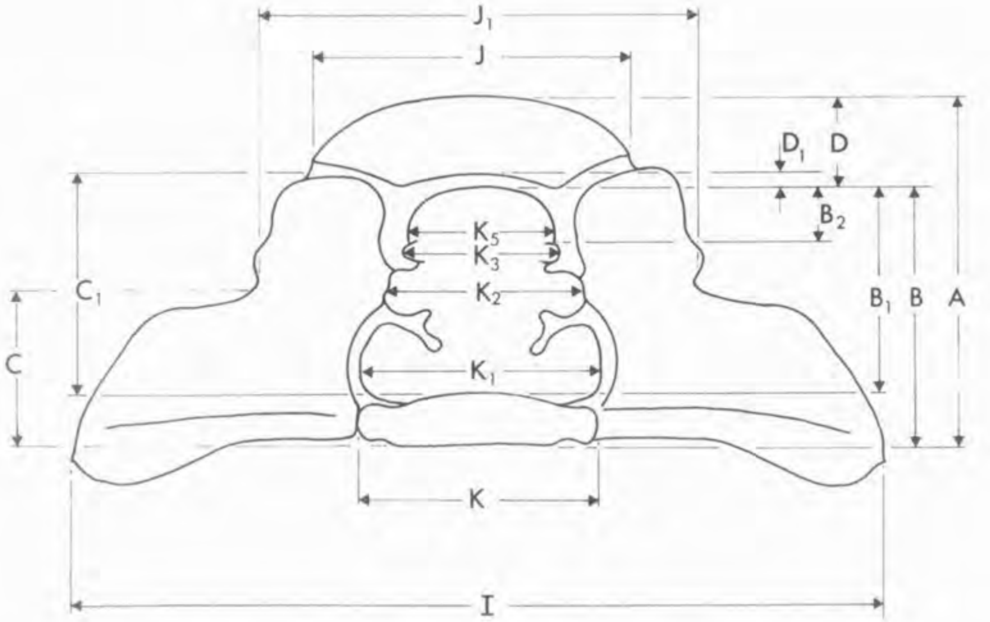
5) Pharostoma foveolatum (Törnquist, 1884) from the middle Ordovician Kullsberg Limestone, Dalarna, Sweden.

6) Reedocalymene expansa Yi, 1957 from the Ordovician (Caradocian) of Fenhsiang area, Ichang, Hupei province, Yangtze-Gorge, China.

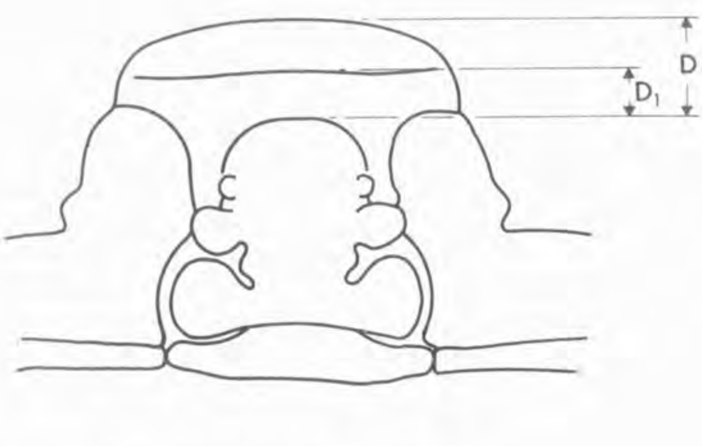
7) Calymenesun tingi (Sun, 1931) from the Ordovician Neichia group of Shihtzupu, Kweichou, China. The Neichia Fauna is regarded by Kobayashi (1951, p. 56) as partly Llanvirn, but mostly early Llandeilo, in age.

The presence of a proboscis in various calymenid genera has been the subject of comment by other palaeontologists (Kobayashi 1951, 1960; Reed 1917; Tillman 1960; Tomczykowa 1970; Whittington 1971); here an attempt is made to discuss the form of this feature in all these examples and to trace, in some of them, its origins. A detailed taxonomic discussion will be given to the Silurian species in the systematic part of this chapter and some of the other taxa mentioned, for example P. foveolatum and Gravicalymene capitovata sp. nov., will be dealt with more fully elsewhere.

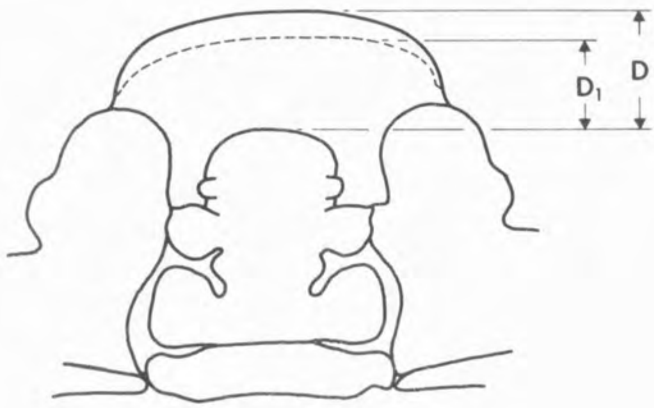
TERMINOLOGY. The terminology employed is largely that used in the Treatise of Invertebrate Palaeontology (Moore 1959, pp. O 117 - O 126). When the preglabellar area is divided into a (posterior) preglabellar furrow and anterior border by a sharp break in slope ('ridge' of Shirley, 1936, p. 390), such as is seen in species of Diacalymene, there is little difficulty in the use and limits of these terms. Where the preglabellar furrow passes forwards and upwards on its anterior side without a sudden, angular break in slope, there is a problem in defining exactly where this side of the furrow ends and the anterior border begins. However, calymenids often lack tubercular ornament (which is present on the rest of the cranidium) in the preglabellar furrow, and I have used this as a guide to the division between this furrow and the anterior border. The term



MEASUREMENTS TAKEN ON CRANIDIUM OF
Tapinocalymene volsoriforma
TEXT-fig. 8A



Tapinocalymene vulpecula
TEXT-fig. 8B



Tapinocalymene nodulosa

TEXT- fig. 8C

preglabellar field does not apply to any of the examples considered with the exception of Pharostoma, where it separates preglabellar furrow from anterior border furrow. The glabella is taken to include the occipital ring unless stated otherwise. The terms 'doublure sector' and 'border sector', used for the inner and outer portions respectively of the rostral plate, and 'cincture', used for the peripheral impression on the pleural region of the pygdidium which marks the position of the cephalic lateral border during enrollment, are all taken from Campbell (1967).

MEASUREMENTS. See Text-figs. 8A - 8C for measurements taken on the cranidium of Tapinocalymene; definitions of these are given in the first part of this thesis. Measurements taken on the pygidium, hypostome and rostral plate are the same as those illustrated and defined in the first part of this thesis.

MORPHOLOGY AND EVOLUTION OF THE PROBOSCIS IN:

1) Tapinocalymene gen. nov.

In 1933 Shirley (p. 53) erected the new specific name of nodulosa for Calymene tuberculosa of Salter, 1848. That this species was distinct from C. tuberculosa Dalman, 1827 was first recorded by Lindström (1885, p. 66). Kegel (1927, pp. 618-19, text-fig. 2f) placed C. tuberculosa Salter non Dalman in his subgenus Diacalymene because of its deep preglabellar furrow and prominent anterior margin. Shirley later (1936, p. 393) emended the concept of Diacalymene and raised it to generic rank, but excluded nodulosa because it lacked the "ridge on the preglabellar field" - a diagnostic character well shown by the type species, D. diademata (Beyrich, 1846). Although nodulosa is not a Diacalymene, I would suggest that it lies at the end of an evolutionary series which arose from that genus. This line consists of three species, two of which are new, and is here referred to a new genus, Tapinocalymene.

TEXT-FIG. 1. Outlines of cranidia, dorsal and left lateral views of species within Tapinocalymene gen. nov. All figures are x 2.

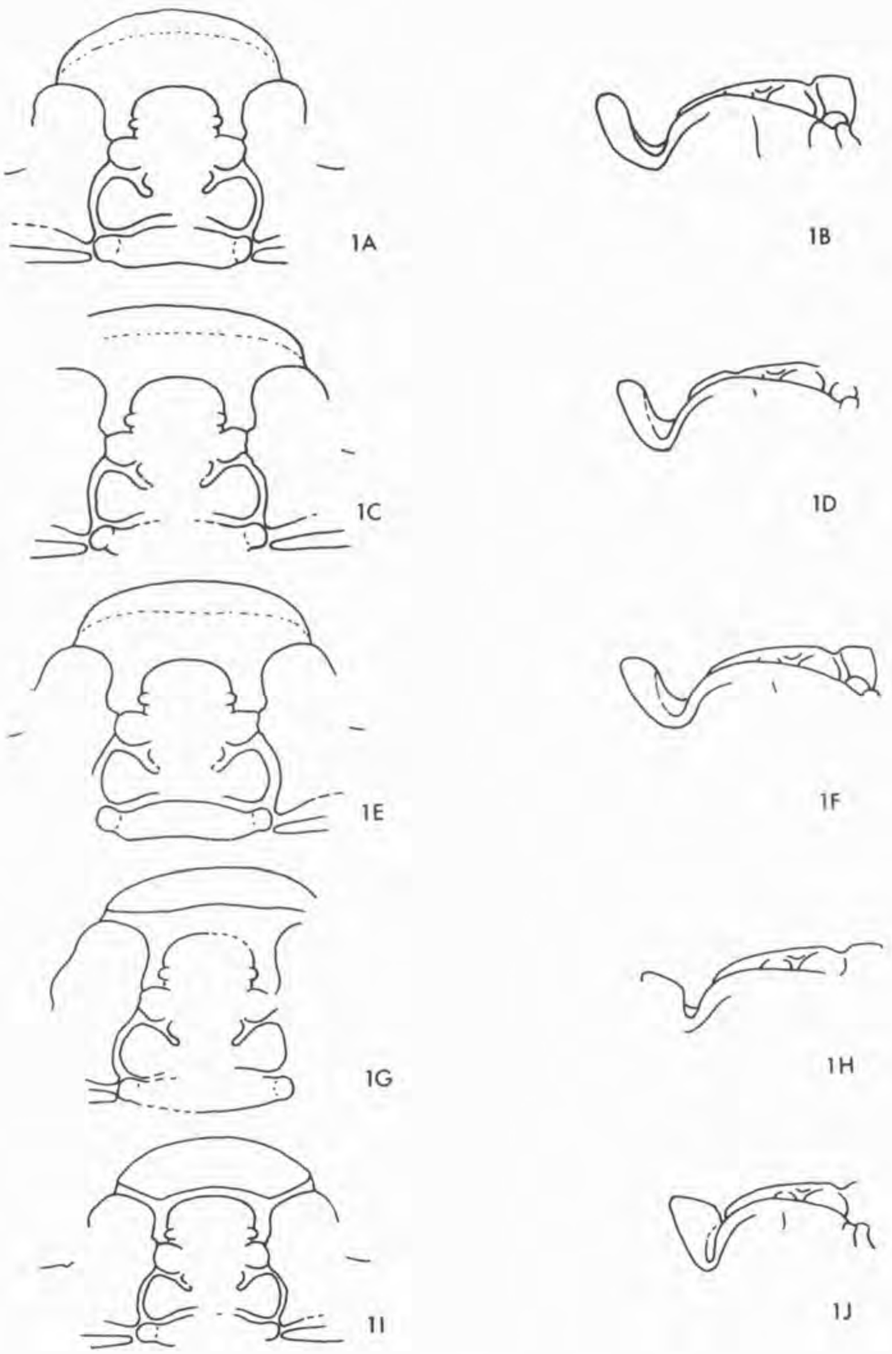
1A-B, T. nodulosa (Shirley, 1933), based on HM A212/1, Wenlock Shale, Durrington, Herefordshire. See Plate 1, figs. 1, 3, 5, 6.

1C-D, T. nodulosa (Shirley, 1933), based on GSM Zs183, Wenlock Shale, Dolyhir, Radnorshire. See Plate 3, figs. 6, 10, 11.

1E-F, T. nodulosa (Shirley, 1933), based on GSM Zs195, Wenlock Shale, Dolyhir, Radnorshire. See Plate 3, figs. 1, 4, 7.

1G-H, T. vulpecula sp. nov., based on the holotype, DJS/48, Wenlock Shale, roadside quarry, quarter of a mile north of Letton, near the Wigmore Rolls area, Herefordshire, Welsh Borderland. See Plate 7, figs. 1, 2, 12.

1I-J, T. volsoriforma sp. nov. based on the holotype, GSM Zs63, probably from the shale band near the base of the Dolyhir Limestone, lowest Wenlock Series, Dolyhir, Radnorshire. See Plate 5, figs. 1-4.



TEXT- FIG.1.

In order of morphological progression, the assigned species to Tapinocalymene comprise:

a) T. volsoriforma sp. nov. from a shale band within the lower Wenlockian Dolyhir Limestone, ? Cyrtograptus centrifugus or Cyrtograptus murchisoni Zones, Dolyhir quarries, Radnorshire.

b) T. vulpecula sp. nov. from the Wenlock Shale, probably C. lundgreni Zone, small disused quarry north of Letton, near the Wigmore Rolls area, Herefordshire.

c) T. nodulosa (Shirley, 1933) which occurs most abundantly in the Wenlock Shale, C. lundgreni Zone, Burrington, Herefordshire.

During its evolution, Tapinocalymene exhibits two main changes in its preglabellar area - an increase in length, and a more marked alteration in its morphology. The overall trend is from the moderately long, ridged preglabellar area of T. volsoriforma, through an intermediate species T. vulpecula, to the longer, scoop-like proboscis of T. nodulosa. The increase in length is accompanied by a decrease in prominence of the ridge separating anterior border from preglabellar furrow, a sagittal lengthening of this furrow, and a shortening of the border itself (Text-fig. 1). The ridge disappears in T. nodulosa, but this species shows intraspecific variation and in some specimens from Dolyhir a relict of the ancestral character can be discerned (see Text-figs. 1C - 1F). This is taken as evidence of the postulated descent. Thus in Tapinocalymene the anterior border is regarded as a progressive evolutionary character.

Tapinocalymene is thought to have originated from Diacalymene because of the similarity of T. volsoriforma,its morphologically most primitive and stratigraphically earliest species, with members of that genus.

Apart from being much longer, the basic form of the proboscis in T. nodulosa is generally the same as the preglabellar area of many Calymene species. If, as seems likely, Diacalymene gave rise to

TEXT-FIG. 2. Outline of cranidium, dorsal and right lateral views of Diacalymene allportiana (Salter, 1865), x 2, based on the holotype, BM 58984, Wenlock Limestone, Dudley, Worcestershire.

TEXT-FIG. 3. Outlines of cranidia, dorsal and right lateral views of Spathacalymene nasuta (Ulrich, 1879) and Diacalymene vogdesi (Foerste, 1887).

3A-B, S. nasuta (Ulrich, 1879), x 1, based on USNM 170363, quarry 0.8 of a mile due east of Napoleon, Indiana, U.S.A; fig. 3A is after Tillman, 1960, pl. 116, fig. 8. See Plate 8, figs. 1-3, 5.

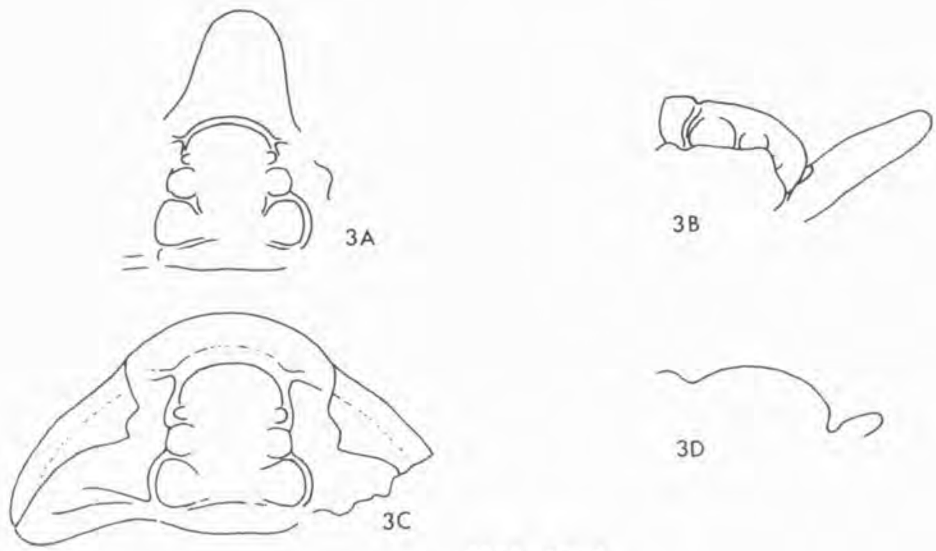
3C-D, D. vogdesi (Foerste, 1887), based on the holotype, Clinton group (sensu Foerste), ? Allen's Quarry, Centreville, Ohio, U.S.A; after Foerste 1887, Plate 8, figs. 12, 13. Magnification of figures unknown, but are equal to Foerste's originals. Figure 3D is a sagittal profile.

TEXT-FIG. 4. Outlines of cranidia, dorsal and right lateral views of species within Palacalymene gen. nov.

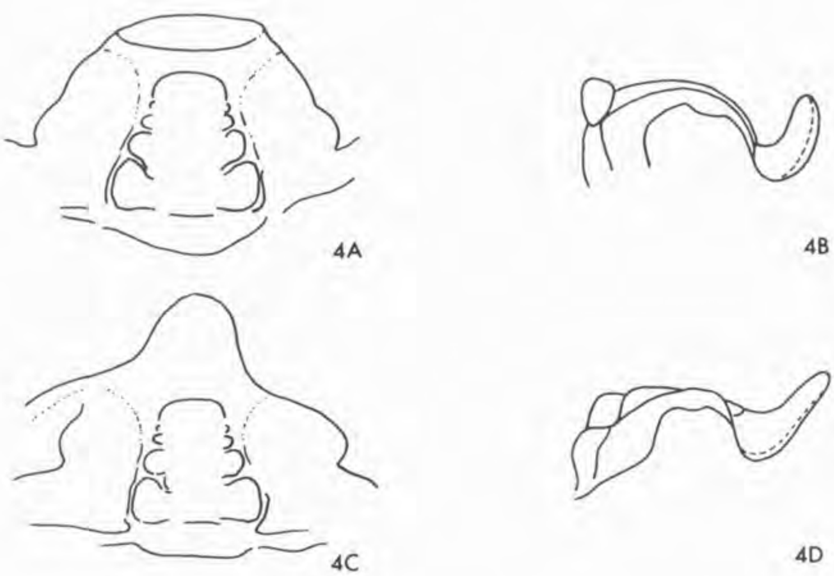
4A-B, P. flexuosa (Tomczykowa, 1970), based on the holotype, IG. 1169. 11. 7, S. leintwardinensis Zone, Ludlovian, Mielnik borehole, Poland. after Tomczykowa, 1970, pl. 2, fig. 5a, p. 74, text-fig. 4d.

4C-D, P. linguata (Tomczykowa, 1970), based on the holotype, IG. 1169. 11. 5, C. hemiaversus Zone, Mielnik borehole, Poland; after Tomczykowa, 1970, pl. 4, fig. 9a, p. 74, text-fig. 4g.

TEXT-FIG. 2.



TEXT-FIG. 3.



TEXT-FIG. 4.

Calymene (see Whittington 1971, p. 457, text-fig. 1), and we have the latter genus present in Llandovery strata (for example C. planicurvata Shirley, 1936 and C. frontosa Lindström, 1885), then species with a non-ridged type of anterior border appear to have developed from Diacalymene at least twice in its history.

2) Spathacalymene Tillman, 1960

The proboscis of S. nasuta has an inverted U-shaped outline, and is composed of a long anterior border, the sides of which slightly diverge posteriorly and the dorsal surface of which slopes downwards posteriorly to meet a sagittally narrow, deep, trench-like preglabellar furrow (see Text-figs. 3A-B and Pl. 8). Tomczykowa (1970, p. 73) believed the proboscis in S. nasuta to be the result of an "expansion of the frontal (= preglabellar) area". I am inclined to the view of Tillman who regarded it as being formed by a prolongation of the anterior border.

Tillman did not suggest any possible origins for his monotypic genus, but, although greatly extended in length, the form of its proboscis closely agrees with the preglabellar area of Diacalymene. Except for its much deeper preglabellar furrow, in sagittal profile the cranidium of T. nasuta is not unlike specimens of D. crassa Shirley, 1936 from the Rhuddanian (lower Llandovery) of Wales, a Diacalymene with a moderately long anterior border. Other cranidial features are also similar - a relatively convex (both transversely and sagittally) high glabella, the frontal lobe of which slopes steeply downwards reaching into the preglabellar furrow. The inner, anterior corner of the fixed cheek in nasuta is rather pointed and overhangs the most anterior part of the lateral border furrow (Pl. 8, fig. 3). This character has also been observed in D. crassa and other species of Diacalymene.

It is therefore worthy of note that Diacalymene sp. aff. D. consimilis (Cooper, 1930) and Diacalymene sp. have been recorded from the Llandoverian part of the White Head Formation, Perce Region, Quebec (Lesperance in

Ayrton et al. 1969, p. 478, table 5), and D. schucherti (Twenhofel, 1928) from the Jupiter Formation (upper Llandovery) of Anticosti Island (Bolton 1972, pl. 9, figs. 3, 9). These records bear witness to the existence of Diacalymene in N America during lower Silurian times. Even more pertinent is the unrevised American species Calymene vogdesi Foerste, 1887. From the illustrations and descriptions of Foerste (1885, pp. 109-12, pl. 8, ? fig. 24, fig. 25; 1887, pp. 95-98, pl. 8, figs. 12-16; 1893, p. 526, pl. 25, ? fig. 24, fig. 25, pl. 27, figs. 12-15) this species is best referred to Diacalymene and, incidentally is remarkably close to crassa, especially in its well rounded frontal lobe and long anterior border. The type specimen of vogdesi appears to come from the Clinton Group (sensu Foerste), ? Allen's Quarry, Centreville, Ohio (Foerste 1885, p. 74; 1887, p. 98; 1893, p. 527, pl. 25, fig. 25, pl. 27, figs. 12, 13). Foerste (1923, p. 41) later used the name Brassfield for the strata he formerly included in his series of papers on the Clinton Group of Ohio, and he (1919, p. 393) regarded vogdesi as a "typical Brassfield species". 'Brassfield' as used by Foerste can include beds of Middle to Upper Llandovery (B_1 - C_2 brachiopod zones) age (after Berry & Boucot 1970, p. 127). Significantly, Foerste (1893, p. 527) also records vogdesi from Hanover, Indiana, the same State that has provided all known specimens of the upper Llandovery species, S. nasuta.

Whittington (1971, p. 457, text-fig. 1, p. 459) suggested that Spathacalymene was derived from Calymene; it is advocated here that it descended directly from Diacalymene. The evolution of Spathacalymene from Diacalymene involves the development of a ridged proboscis with a very long anterior border, from a ridged preglabellar area with only a moderately long anterior border. The anterior border and preglabellar area of 'C'. vogdesi are, respectively, just greater than one fifth and one quarter as long as the glabella (measured from Foerste, 1893, pl. 27, fig. 12 - the holotype); in S. nasuta these proportions are about three quarters and four fifths (measured from USNM 170363). If this lineage is accepted, compared to the trend postulated in Tapinocalymene, the evolution of the proboscis here involves much less change in morphology and a considerably greater increase in length, from ancestor to descendant.

3) Palacalymene gen. nov.

Palacalymene flexuosa (Tomczykowa, 1970), Palacalymene linguata (Tomczykowa, 1970) and Palacalymene brevis (Tomczykowa, 1970) from the middle Ludlovian of Poland all exhibit a proboscis which is from less than one half (P. brevis) to about two-thirds (P. linguata) as long as the glabella, though these lengths can vary somewhat within a single species (Tomczykowa, 1970, pp. 79, 83). Measurements taken directly from Tomczykowa's plates also indicate that these proportions do not include the occipital ring as part of the glabella. The proboscis of Palacalymene is produced forwards and weakly to strongly upwards, but it is debatable as to which part of the cranidium is responsible for its formation. As Tomczykowa recognised it is difficult to distinguish the division between preglabellar furrow and anterior border, though she described this furrow as "wide and shallow" in P. linguata.

In all three species of Palacalymene, rather coarse tubercles are present on the proboscis almost up to the anterior margin of the frontal glabellar lobe (see Tomczykowa 1970, pl. 1, fig. 7a, pl. 2, figs. 5a, 6a, 7a, pl. 3, fig. 16a, pl. 4, figs. 7a, 9a). As calymenids normally lack (or at the most have only very fine, sparsely distributed) tubercles in the preglabellar furrow, but have them present on the anterior border (see T. nodulosa, Pl. 4, fig. 1, Pl. 5, figs. 1, 5, 6 and T. mammillata in Whittington 1971, pl. 1, figs. 4, 5, 7), this suggests the latter feature forms the proboscis in the Polish species. The preglabellar furrow would then be limited to a very narrow strip in front of the glabella, and the presence of such a strip is indicated on some of Tomczykowa's illustrations (pl. 5, figs. 10a, 10b, 12b).

The derivation of Palacalymene remains uncertain, but the lack of a papillate - buttress structure in this genus and the nature of its glabella and lobation indicate that it is most closely related to Gravicalymene, Thelecalymene and Flexicalymene. The nature of the development of the proboscis in the new genus is obviously dependent on which, if any, of these genera provided the ancestral stock. A derivation from Flexicalymene would require the least alteration in the preglabellar area from ancestor to descendant.

4) Thelecalymene Whittington, 1971

T. mammillata (Hall, 1861) has a proboscis about half as long as its glabella and is composed of a sagittally long, shallow preglabellar furrow and a gently sloping anterior border (preglabellar field of Whittington 1971, p. 134). The anterior border and preglabellar furrow are of about equal sagittal length (measured from Whittington, pl. 1, figs. 4, 5, pl. 2, fig. 1), and the anterior margin of the proboscis is well rounded in outline.

The glabella of Thelecalymene, with the exception of its unusual papillate frontal glabellar lobe, is very similar to that of Gravicalymene, and although the preglabellar areas of both genera are generally unalike, the boss on the proboscis of Thelecalymene is strongly reminiscent of the pronounced ridging in the same position (opposite the axial furrow) in many Gravicalymene species (Whittington 1971, p. 130). Consequently the belief (Whittington 1971) that Thelecalymene is most closely related to Gravicalymene is shared by the present author. Gravicalymene is represented in N America in contemporaneous and older rocks to those yielding Thelecalymene (see Ross 1967). Of material I have studied from NW Europe a new taxon from the middle Ordovician Ogygiocaris Shale (division 4aα 3) of the Oslo Region shows a close resemblance in several characters to T. mammillata, and as much

TEXT-FIG. 5. Outlines of cranidia, dorsal and left lateral views of Thelecalymene mammillata (Hall, 1861) and Gravicalymene sp. nov. All figures are x 2.

5A-B, T. mammillata (Hall, 1861), based on MCZ 8672/2, Elgin Shaley Limestone Member, Maquoketa Shale, 0.25 miles south-west of Graf, Dubuque County, Iowa; after Whittington, 1971, pl. 1, figs. 2, 4.

5C-D, Gravicalymene sp. nov., based on a cast of the external mould of holotype, PMO 91061, Ogygiocaris Shale, Muggerudkleiva, Eiker-Sandsvaer district of the Oslo Region, Norway. Figure 5D is a sagittal profile.

TEXT-FIG. 6. Outlines of cranidia, dorsal and right lateral views of Pharostoma foveolatum(Törnquist, 1884) and Pharostoma simile Thorslund, 1940.

6A-B, P. foveolatum x 1, based on IPU Ar469, Kullsberg Limestone, Dalarna, Sweden.

6C-D, P. simile, x 2, based on IPU Ar2468, T56, Lower Chasmops Limestone, Tvären, Södermanland, Sweden.

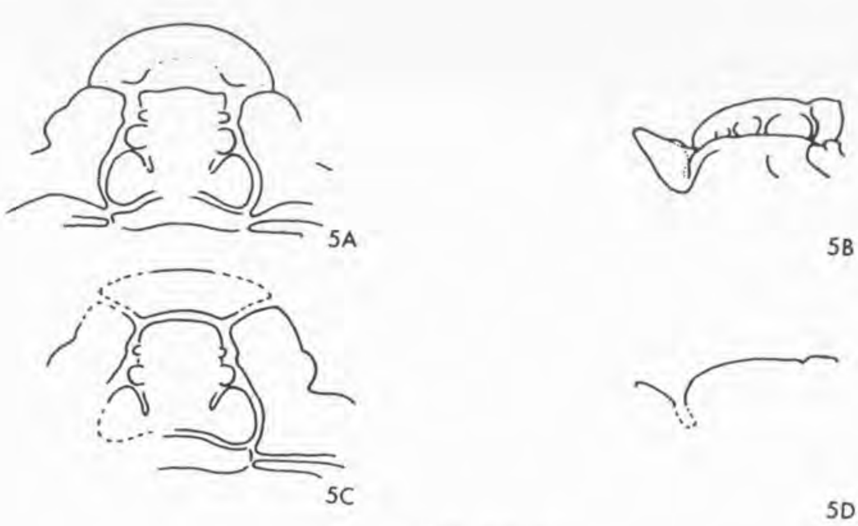
TEXT-FIG. 7. Outlines of cranidia, dorsal views of Reedocalymene expansa Yi, 1957, Reedocalymene expansa var brevica Yi, 1957 and Calymenesun tingi (Sun, 1931).

7A, R. expansa, x 1.5, based on one of the original syntypes, Ordovician of the Fenhsiang area, Ichang, Hupei province, China; after Yi, 1957, pl. 1, fig. 1b.

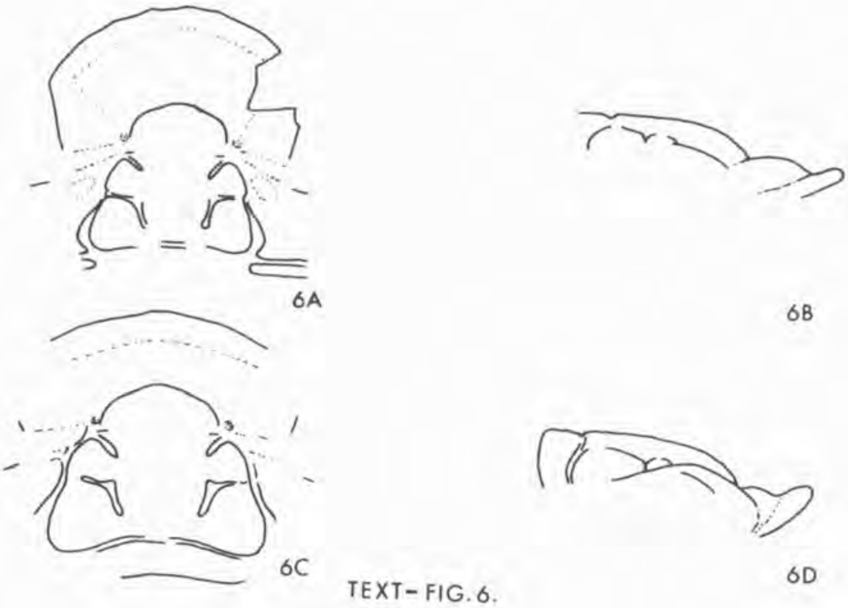
7B, R. expansa var. brevica, x 2, based on one of the original syntypes, same horizon and locality as for fig. 7A; after Yi, 1957, pl. 1, fig. 2b.

7C, C. tingi, x 1.5, based on syntype in Geol. Surv. China, middle Ordovician Hiechia group, Shihtzupu, Kweichou, China; after Sun, 1931, pl. 3, fig. 9f.

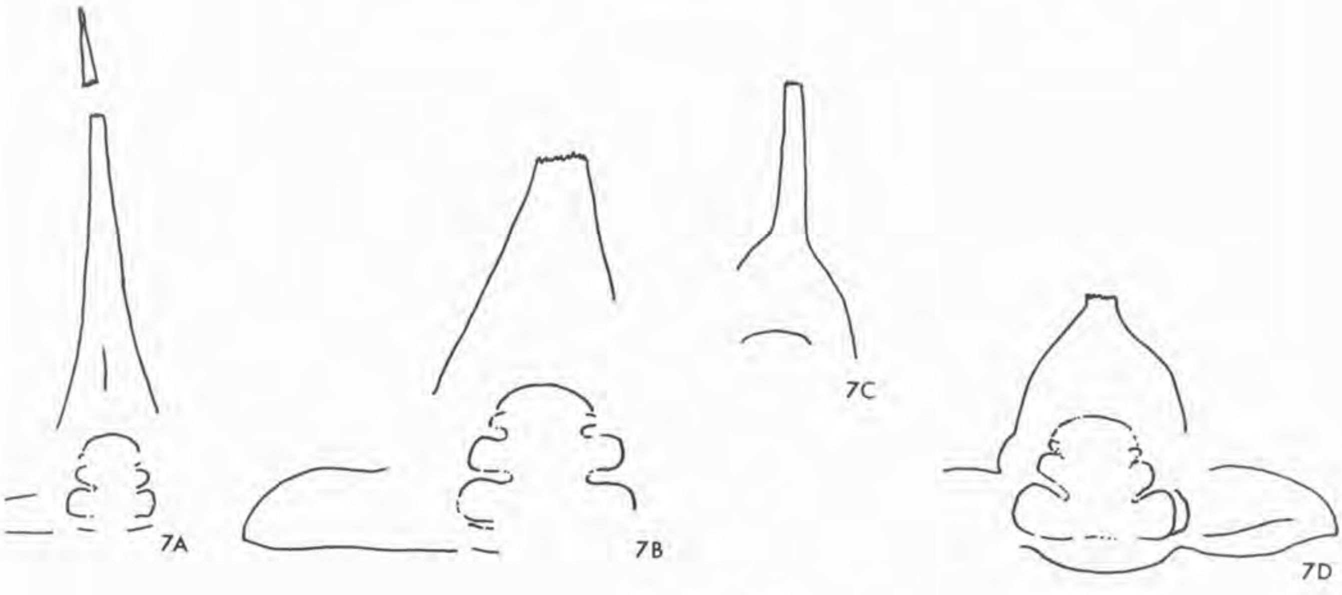
7D, C. tingi, x 2, based on syntype in Geol. Surv. China, same horizon and locality as fig. 7C; after Sun, 1931, pl. 3, fig. 9d.



TEXT-FIG. 5.



TEXT-FIG. 6.



TEXT-FIG. 7.

as any other Gravicalymene species serves to indicate the close relationship of the two genera. Particular features common to both T. mamillata and G. capitovata sp. nov. include a somewhat short glabella, very large basal glabellar lobes, the remnant of an eye ridge on the abaxial margin of the axial furrow, and a slight overhang of the anterior part of the fixed cheek over the border furrow (Text-fig. 5).

If Thelecalymene was derived from Gravicalymene, to account for the dissimilarity in their preglabellar areas an evolutionary trend involving the loss of the ridge separating anterior border from preglabellar furrow, and a lengthening of this furrow would be necessary. This trend is comparable to the sequence from T. volsoriforma to T. vulpecula and it appears one has a similar type of evolution in the preglabellar area of both buttressed and non-buttressed calymenids (compare Text-figs. 5A-D with Text-figs. 1A-B and 1I-1J).

5) Pharostoma Hawle & Corda, 1847.

The proboscis of P. foveolatum (Törnquist, 1884) is largely formed by a sagittally and transversely convex preglabellar field which can be up to half as long as the glabella; its anterior margin is strongly arched as in T. mammillata. P. foveolatum probably descended from Pharostoma simile Thorslund, 1940 from the Lower Chasmops Limestone of Södermanland, Sweden - a species which has many cranidial characters the same as in the younger Kullsberg Limestone taxon, and with a preglabellar field of similar morphology but only about a quarter as long at its glabella (Text-fig. 6). In this trend, and also that of Spathacalymene, the amount of structural change in the preglabellar area from ancestor to descendant is minimal; only an increase in the length of existing morphological features is involved.

6) and 7) Reedocalymene Kobayashi, 1951 and Calymenesun Kobayashi, 1951.

Reedocalymene and Calymenesun, two closely related non-buttressed genera, both have a very long proboscis. In the type species of Reedocalymene, R. unicornis (Reed, 1917) from the Ordovician, ? Llanvirn (see Dean 1967, p. 23) of Pu-piao, Yunnan, it is at least twice the length of the glabella (measured from Reed 1917, pl. 8, figs. 10, 10a), and may be longer as the extreme anterior margin of Reed's specimen seems to be missing. In the stratigraphically younger R. expansa Yi, 1957 from the Caradocian of the Yangtze - Gorge, China, the proboscis can reach up to about four times as long as the glabella (measured from Yi 1957, pl. 1, fig. 1b; see Text-fig. 7A). In both these species of Reedocalymene the proboscis is spatulate-like in outline, comprising a broad posterior inflation which is followed anteriorly by a narrow medial ridge. Calymenesun tingi (Sun, 1931) from the Ordovician, ? Llandeilo, of China also has the posterior part of its preglabellar area broadly swollen, but the outline of which tapers more sharply anteriorly than in Reedocalymene, and it is then extended in the form of a long narrow spine (see Sun 1931, p. 29, pl. 3, figs. 9a-9f; Sheng 1958, p. 201, pl. 7, fig. 4a; herein Text-figs. 7C, 7B).

From existing illustrations and descriptions, it is difficult to assess which part of the cranidium gives rise to the proboscis in Reedocalymene and Calymenesun. The inflated area immediately in front of the glabella in both these genera is similar to the preglabellar field of Pharostoma or Neseuretus (Neseuretinus), but it can only be regarded as a true preglabellar field if it is confined posteriorly by a preglabellar furrow, and anteriorly by an anterior border furrow. Both genera have a preglabellar furrow, but I am uncertain as to whether they have a definite anterior border furrow. Kobayashi (1951, p. 44) described the preglabellar area of C. tingi as being "interrupted by a shallow concavity through the marginal border" which may in fact represent a very weak anterior border furrow. If this is so then most of the proboscis in Calymenesun is formed by a very long anterior border which lies in front of the border furrow. There is no mention of an anterior border furrow in descriptions of Reedocalymene, though there appears to be a shallow depression in front of the posteriorly sited inflation in some of the specimens (see Yi 1957, pl. 1, figs. 1a, 1b.); this would mean the proboscis was also formed in this genus essentially by an extended anterior border. However as there is no distinct anterior border furrow in either Reedocalymene or Calymenesun, it is perhaps best to regard the proboscis in each of these genera as being formed by a long undivided preglabellar area, the anterior border and preglabellar field of which are coalesced in the same fashion as that proposed for species of Neseuretus (Neseuretus) by Whittard (1960, p. 143).

There can be no doubt that both Reedocalymene and Calymenesun are closely related to Neseuretus Hicks, 1873, from which they probably descended, and species of which are present in the Llanvirn of China and possible Llandeilo or early Caradoc of the Himalayas (see Kobayashi 1951, p. 56, and 1960, p. 43; Dean 1967, pp. 20-21).

THE FUNCTION OF A PROBOSCIS

The different types of proboscis discussed herein almost certainly served a variety of functions. In most of the genera the projection probably arose in response to a high degree of adaptive specialization to a new mode of life or ecological niche.

Tillman (1960, p. 893) suggested that an "anterior process", such as that of S. nasuta, may have acted as a counterweight to keep the posterior part of the body off the sea bottom during feeding, or where both anterior process and genal spines were present, to aid general stability. Alternatively the proboscis of nasuta may have helped streamline the trilobite for increased speed of movement.

The shovel-like proboscis of T. nodulosa appears ideally shaped to function as a scoop - perhaps for disturbing loose sediment in search of food, or to facilitate shallow burrowing, for it is reasonable to assume that this species had a benthonic habit. There are at least two other possible uses: It may have been an adaptation for ploughing aside the superficial mud during locomotion. Secondly, the long broad proboscis would have added to the surface area of the trilobite, and this increase would have been a distinct advantage in preventing it sinking into a soft and unconsolidated substrate, which seems likely to have been present in the Wenlock Shale environment.

It is noteworthy that in the Wenlock Shale of Burrington one finds Dalmanites associated with T. nodulosa, and in the Wenlock Shale of Rushbury near Wenlock Edge they are also accompanied by Raphiophorus. All these sympatric taxa have anterior projections, though they are variably developed and almost certainly had different functions.

THE TAXONOMIC SIGNIFICANCE OF A PROBOSCIS IN CALYMENIDS

The discrimination of the different trends outlined above is helpful in the interpretation of calymenid phylogeny. The examples given demonstrate the potential of several calymenids to develop a feature which should be given careful evaluation in classification. Considered in isolation, the amount of information concerning phylogeny that the proboscis can provide may be low, and other characters prove more reliable as indicators of descent. Superficial similarities of the proboscis in different species may induce groupings which cut across natural phyletic lines.

In 1970 Tomczykowa placed T. nodulosa, P. brevis, P. linguata and P. flexuosa all in Spathacalymene. Although S. nasuta and T. nodulosa both have a long proboscis, the morphology of each projection is completely different (compare Pl. 4, fig. 7, with Pl. 8, fig. 1), and

I believe that these two species represent the end members of two separate lineages, each of which evolved its proboscis in a different way (as outlined above).

Likewise, apart from sometimes having a similar outline in dorsal view (compare Text-figs. 3A and 4C), the structure of the proboscis in members of Palacalymene is quite distinct from that of S. nasuta, in addition to which many other features separate the Polish and American species, and they are not regarded here as congeneric.

In curving forwards and upwards and having no ridge dividing anterior border from preglabellar furrow, the proboscis in Palacalymene, particularly in P. flexuosa, is not unlike that of T. nodulosa (compare text-figs. 1B and 4B). Other characters are comparable in the British and Polish species, but they are also not regarded as congeneric (see generic discussion below), and their similarity is thought to be the result of convergence.

It is arguable whether the proboscis of the species nasuta is sufficient to justify its separation from Diacalymene at the generic level. A case could be made for regarding the American taxon as a subgenus of Diacalymene characterized by a very long anterior border. After all, the difference between nasuta and members of Diacalymene is roughly equivalent to that between P. foveolatum and members of Pharostoma, and foveolatum has not been separated even at the subgeneric level.

SYSTEMATIC PALAEONTOLOGY

Family CALYMENIDAE Milne Edwards, 1840

Subfamily CALYMENINAE Milne Edwards, 1840

Genus TAPINOCALYMENE gen. nov.

DERIVATION OF THE NAME. From the Greek tapeinos, humble, alluding to the nature of the glabella which is sunk fairly low and is short in relation to the fixed cheeks.

TYPE SPECIES. Calymene nodulosa Shirley, 1933, p. 53, pl. 1, figs. 6-10; from the Wenlock Shale, Burrington, Herefordshire.

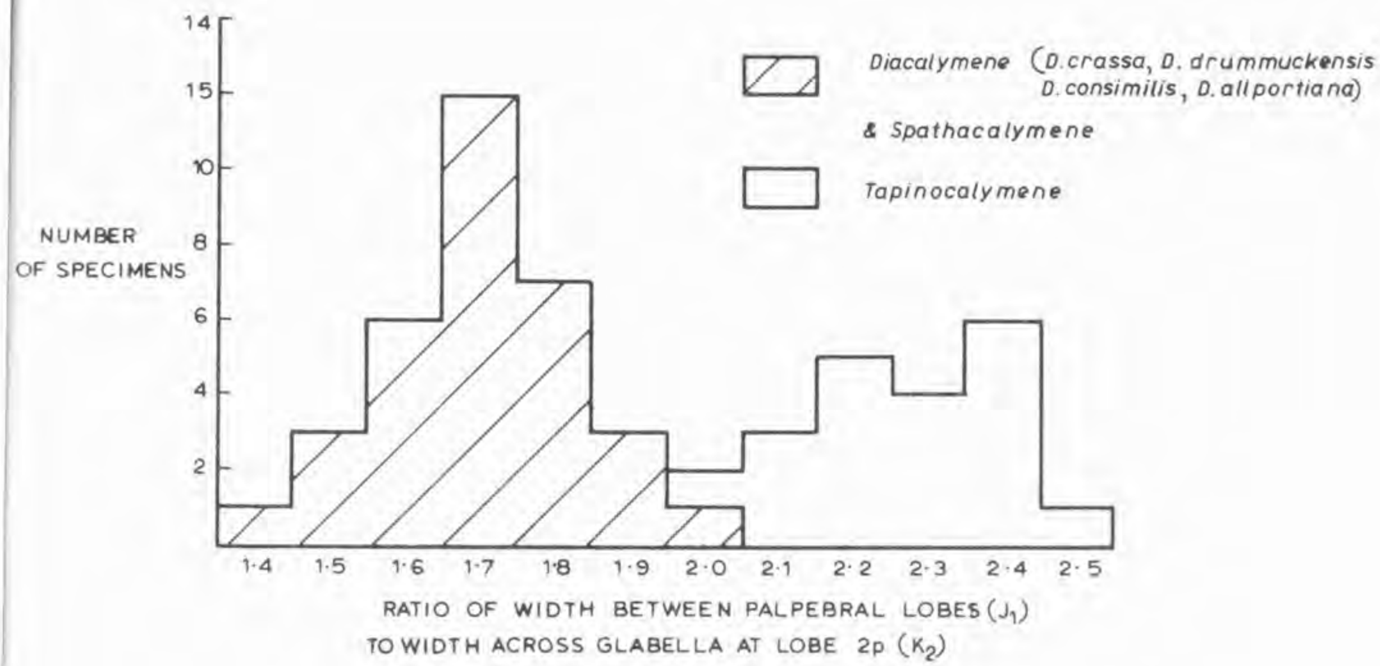
OTHER SPECIES. T. volsoriforma sp. nov.; T. vulpecula sp. nov.

DIAGNOSIS. Preglabellar area relatively long, though variably developed. In dorsal view, glabella does not protrude in front of fixed cheek, more often than not lies well behind it; in lateral view, dorsal surface of glabella stands only just above fixed cheek, is sometimes below fixed cheek anteriorly. Lateral lobe 2p is bridged across axial furrow to a genal buttress. Palpebral lobes are from twice to 2.5 times as wide (tr.) apart as width of glabella at 2p lateral lobes. Hypostome has moderate to prominent ventrally directed projection on anterior lobe; maculae are large and ovate; posterior border is expanded into flat, moderately long spines. Pygidial axis almost flat (tr.); inner pleural region slopes gently abaxially; interpleural furrows are weak or obsolete. Small to medium sized tubercles uniformly distributed on glabella; anterior adaxial part of fixed cheek and often anterior border have much larger tubercles.

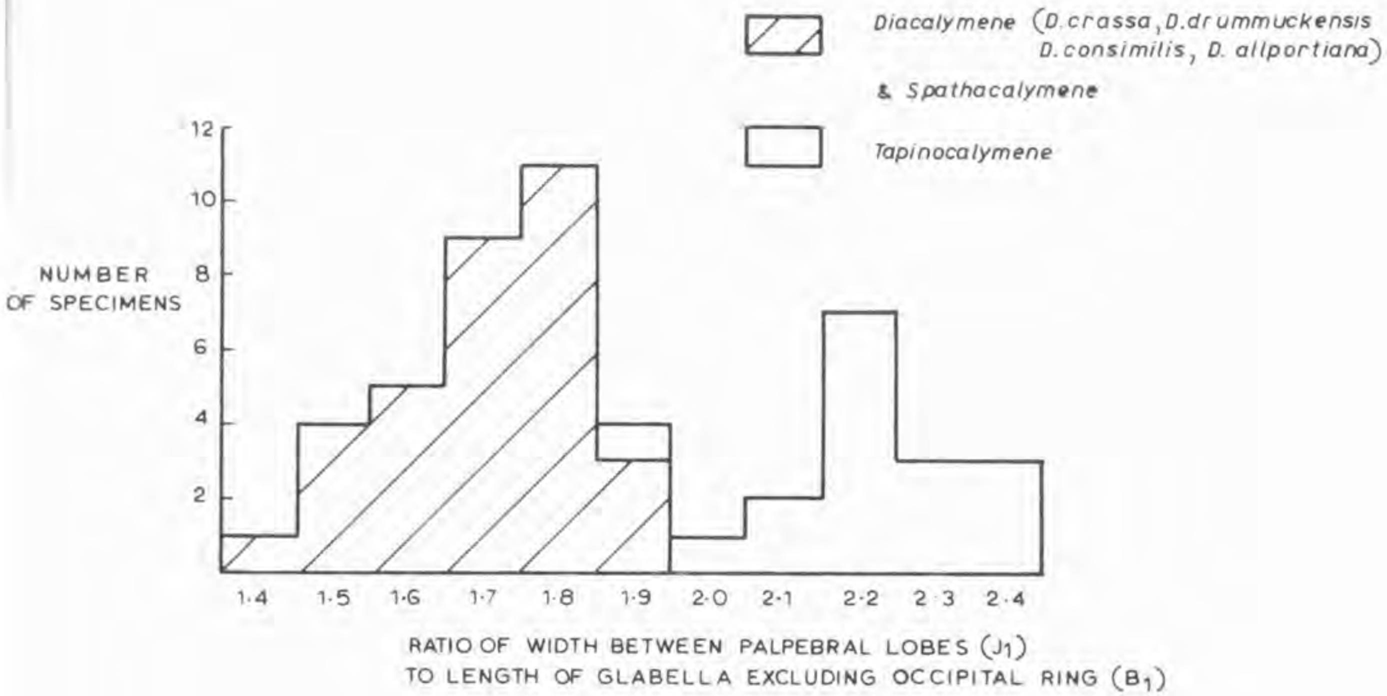
DISCUSSION. Since 1936 many authors have followed Shirley's thesis that specimens showing a ridged or 'thickened' anterior border and a papillate 2p lateral glabellar lobe joined to an adaxially projecting genal buttress should be placed in Diacalymene; and that those species with this bridge across the axial furrow but without the ridged preglabellar area should be placed in Calymene. This classification is for the most part employed by the present author but it was found difficult to use when considering T. nodulosa, T. volsoriforma and T. vulpecula. All three species have the axial furrow bridged at 2p lateral lobe, but volsoriforma and vulpecula possess a Diacalymene type of anterior border, whilst nodulosa displays a type diagnostic of Calymene. However, these three species all have in common a number of distinct characters which weigh heavily against placing nodulosa in a separate genus, and which differ and enable their separation from both Diacalymene and Calymene.

The anterior border in Tapinocalymene is evolving quite rapidly, and is useful for specific discrimination, but not for diagnosing the genus. The former unifying role of the anterior border as a more stable generic character (as in Diacalymene) is now adopted by other morphological features. None of the features in the diagnosis of Tapinocalymene is completely exclusive to the genus, but in particular a short and low glabella, widely separated palpebral lobes, and a distinct style of cranidial ornamentation all combine to separate Tapinocalymene from other papillate - buttressed genera. The form of the glabella in T. nodulosa is unusual for a calymenid of (particularly middle) Silurian age because, in contrast, increased inflation and projection of the glabella above and beyond the fixed cheek was a theme prevalent in calymenid evolution during this time (see Shirley 1936, p. 388). The existence of two other species in the Wenlockian of the Welsh Borderlands with the same type of glabella and overall morphology is taken as significant, and this group of species is sufficiently distinct to be deemed worthy of formal recognition.

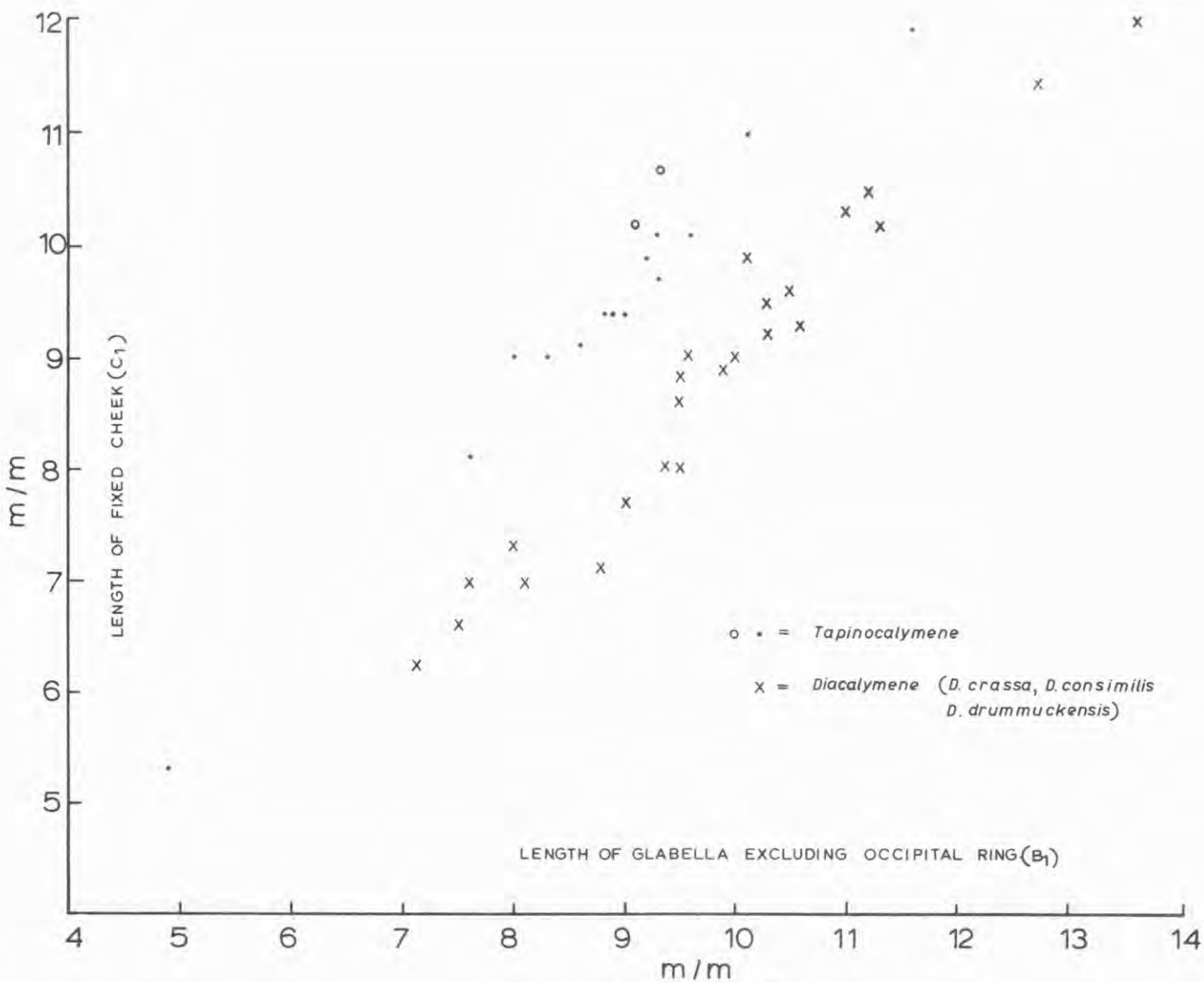
Tapinocalymene differs from Diacalymene in the following ways. In dorsal view the glabella does not reach in front of and more often than not lies behind the fixed cheek; in lateral view the glabellar profile is lower in relation to the height of the fixed cheek - especially anteriorly where it sometimes assumes a position below the cheek. The Diacalymene species I have examined(for example D. diademata, D. drummuckensis, D. crassa) all show a more dorsally protruding glabella which juts (often prominently) beyond the fixed cheek. The palpebral lobes of Tapinocalymene are wider apart (variate J_1) compared to the width of the glabella at lobes 2p (variate K_2); measured specimens range from twice to 2.5 times as wide in Tapinocalymene, but from only 1.4 to twice as



TEXT - fig. 9



TEXT - fig. 10


12
11
10
9
8
7
6
5
m/m
LENGTH OF FIXED CHEEK (C_1)
o • = Tapinocalymene
x = Diacalymene (D. crassa, D. consimilis
D. drummuckensis)
LENGTH OF GLABELLA EXCLUDING OCCIPITAL RING (B_1)
4
5
6
7
8
9
10
11
12
13
14
m/m

TEXT-fig.11

wide in Diacalymene (see Text-fig. 9). The relatively great width separating the palpebral lobes in members of Tapinocalymene appears typical of the whole exoskeleton of T. nodulosa, the only member of the genus of which there are complete individuals extant, but this variate (J) was chosen for comparison as it was the one most often available for measurement. The inner, anterior corner of the fixed cheek of Tapinocalymene has a more rounded outline in dorsal view than in nearly all species of Diacalymene where it is somewhat pointed and projects slightly forwards and inwards. An exception to this distinction is D. gibberosa sp. nov. from the Llandovery of Norway which has been described by me elsewhere; nevertheless the glabellar morphology of gibberosa is totally different to that of Tapinocalymene species and this feature alone generically separates the Norwegian taxon, which is not considered to be one of the Diacalymene species that are close to members of the new genus. Other features characteristic of (but not totally peculiar to) Tapinocalymene include the interpleural furrows, axis, and inner pleural region of its pygidium which are, respectively, extremely weak (Pl. 4, figs. 3, 4, 6; Pl. 3, fig. 5), only very slightly convex (tr.) (Pl. 4, fig. 6; Pl. 2, fig. 2), and gently descending abaxially (Pl. 5, fig. 6). Examples of Diacalymene which show some of these traits include D. diademata Beyrich, 1846 (rather weak inter-pleurals), and D. gibberosa (almost flat (tr.) axis and gently descending inner pleural region).

Species of Tapinocalymene and those species of Diacalymene I have examined which have their cuticle extant all show a similar type of glabellar ornamentation - that is relatively fine to medium sized tubercles which are uniformly distributed and fairly closely spaced. But, with the exception of D. allportiana (Salter, 1865), in Diacalymene the tubercles do not increase in size on the adaxial part of the fixed cheek (especially anteriorly), and genal buttress. D. allportiana is closely related to Tapinocalymene taxa but may be distinguished by its higher glabella which is longer than its fixed cheeks. (see Text-fig. 2).

The hypostome of Tapinocalymene has more swollen maculae than those in the known hypostomes of Diacalymene. The hypostomes of T. vulpecula and T. nodulosa both show a prominent spine-like projection on the anterior lobe, whereas the only known hypostome of volsoriforma appears to have a gently inflated subcircular raised area which is like that of Diacalymene species.

Nearly all Calymene species differ from those of Tapinocalymene in having a more dorsally and anteriorly projecting glabella, glabellar tubercles which are more variable and often larger in size, more narrowly separated palpebral lobes, a steeper slope to the inner pleural region of the pygidium, a more convex (tr.) pygidial axis, and better defined interpleural furrows - particularly distally. All these distinctions apply and are most obvious when comparing members of Tapinocalymene with the Wenlock Limestone species C. blumenbachii Brongniart, 1822 and C. aspera Shirley, 1936.

Some of the features characteristic of Tapinocalymene are occasionally exhibited by species of Calymene - for example C. tuberculosa Dalman, 1827 from the Wenlock Series of Gotland and England has a moderately flat (tr.) pygidial axis, and in C. tenera Barrande, 1852 from the lower Ludlow of Bohemia the interpleural furrows are almost obsolete - but the combined group of features which distinguish the new genus are all present only in T. volsoriforma, T. vulpecula, and T. nodulosa.

C. neointermedia R. & E. Richter, 1954 from the Ludlovian of Gotland has been compared (Schrank, 1970, p. 122; Whittington 1971, p. 463) with T. nodulosa because of the similarity of their long, scoop-like preglabellar area. This species has been discussed in detail by me elsewhere and on account of its glabellar morphology in relation to its fixed cheek, and the style of its cranidial ornament, it is not regarded as congeneric with nodulosa. Rather, neointermedia is considered to be closely related to C. peullaris Reed, 1920, C. lawsoni Shirley, 1962 and C. patustria sp. nov.

C. puellaris also shows a resemblance to nodulosa, and of all the Calymene species has a preglabellar area most like that of the stratigraphically earlier Wenlock taxon; but this resemblance is thought to be the result of parallelism, and C. puellaris a species from yet another calymenid genus which has independantly acquired a long preglabellar area. C. puellaris is distinguished generically from T. nodulosa by the same characters as those which differentiate C. neointermedia.

Diacalymene, Calymene and Tapinocalymene all show a discrete inflation on the anterior lobe of the hypostome. The most extreme form of this inflation - an anteroventrally directed spine-like projection - is known to occur in both Tapinocalymene (T. nodulosa) and Calymene (for example in C. lawsoni), but has not yet been observed in species of Diacalymene.

Tomczykowa (1970, p. 70) has referred nodulosa to Spathacalymene Tillman, 1960, which was previously monotypic, though she recognised that the British Species (and also four other species from Europe that she assigned to Spathacalymene) differed in certain respects from S. nasuta. After examining the type and other material of nasuta, I am convinced that nodulosa does not belong in the American genus.

Tomczykowa gave the following revised diagnosis for Spathacalymene: "Glabella bell-shaped, variably developed U-shaped spatulate process projects from the frontal part of the cranidium. Ocular cheeks high. Rostrum large. Thirteen thoracic segments. Pygidium with five to seven axial rings, four pleural furrows, interpleural furrows faint or obsolete, border anteriorly wide". The presence of a "spatulate process" in nodulosa was without doubt the main reason why it was attributed to Spathacalymene, but the use of this feature as a basis for combining nodulosa and nasuta in the same genus is here regarded as unsound (see above, "The taxonomic significance ..." etc.). Some of the differences between these two species have been given previously; S. nasuta is further distinguished from nodulosa by having a very convex (sag. & tr.) glabella which projects beyond and well above its fixed cheeks, more narrowly separated palpebral lobes, a more V-shaped rostral suture, a pointed inner anterior corner to its fixed cheek, a relatively narrower pleural region to its thorax and pygidium, and by lacking coarse tubercles on the inner part of its fixed cheek (compare Pls. 4-7 with Pl. 8).

Where equivalent exoskeletal material of T. vulpecula and T. volsoriforma is available for comparison with that of S. nasuta, they are seen to be distinguished from the American species by the same characters as those which distinguish nodulosa. Many of these characters are incorporated in the generic diagnosos of Tapinocalymene.

Papillicalymene Shirley, 1936 from the Ludlovian of Gotland has a very advanced type of genal buttressing and papillation of the lateral glabellar lobes which easily differentiate it from Tapinocalymene.

OCCURRENCE. From near the base to near the top of the Wenlock Series, (possibly C. centrifugus or C. murchisoni zones of the C. lundgreni or perhaps the M. ludensis Zone), in the Welsh Borderlands and Wales.

Tapinocalymene volsoriforma sp. nov.

Plate 1; Plate 2, figs. 1-7, 9, 10; Text-figs. 1I-J.

1918 Calymene blumenbachii Brongniart; Reed in Garwood & Goodyear, p. 19.

DERIVATION OF THE NAME. Popular Latin, volsorium, the stone of an arch with its sides inclined towards each other, and forma, shape, referring to the outline of the anterior border in dorsal view.

HOLOTYPE. An almost complete cranidium; GSM Zs63, Garwood Collection; Pl. 1, figs. 1-4.

TYPE STRATUM AND TYPE AREA. Wenlock Series, the thin shale band included within the Dolyhir Limestone near its base, Dolyhir Quarries, near Old Radnor, Radnorshire (see Garwood & Goodyear 1918, p. 18, pl. 7).

Specimens of this species, including the holotype, in the Garwood Collection of the Geol. Surv. Mus. have no precise locality or (particularly) stratum information other than "Dolyhir", but apart from the Pre-Cambrian, only the Dolyhir Limestone and a small patch of Wenlock Shale are known to outcrop in this area. The Wenlock Shale at Dolyhir is lithologically different to the matrix surrounding the T. volsoriforma specimens and is known to yield a different species of Tapinocalymene (see discussion of T. nodulosa). This matrix is also unlike the mass of pure crystalline Dolyhir Limestone though Garwood & Goodyear (1918, p. 18) record a shale band included in the Limestone near its base, and their description of this band is applicable to the Geol. Surv. Mus. material. The proposal that this horizon provided Garwood & Goodyear's specimens of T. volsoriforma is supported by the present author's collection of a poorly preserved cranidium (DJS/82) of the species from the shale band at one of their localities - on the north side of the old railway track, south-east of their quarry 'E' (Nat. Grid. Ref. SO 2410 5823).

No exact type locality is designated as the shale band outcrops in several quarries in the Dolyhir area and it is not known which one furnished the holotype.

The age of the Nash Scar Limestone, lateral equivalent of the Dolyhir Limestone, is given by Cocks, Holland, Rickards and Strachan (1971, p. 109, fig. 2) to include the C. centrifugus, C. murchisoni and part of the M. riccartonensis graptolite zones of the lowermost

Wenlock Series. However, they equate the upper and lower age limits of this limestone with these standard zones with some degree of uncertainty, and Zeigler, Cocks and McKerrow (1968, p. 750) have previously suggested that part of the Nash Scar Limestone could possibly be as old as Upper Llandovery (C_3). The shale band near the base of the Dolyhir Limestone is therefore tentatively regarded as centrifugus or murchisoni Zone in age.

ADDITIONAL MATERIAL. At least three incomplete cranidia, GSM Zs62, GSM Z19983, LM 2850; one incomplete cranidium and its left free cheek, GSM Zs65; one incomplete cephalon and its rostral plate GSM Zs58; seven incomplete pygidia GSM Zs22, GSM Zs24, GSM Zs57, GSM Zs59-61, GSM Zs64; one incomplete hypostome GSM Z19696. Numerous other fragments of cranidia, pygidia and thoracic segments are present in the Garwood Collection, Geol. Surv. Mus.

DIAGNOSIS. Preglabellar area about one third as long as glabella. Preglabellar furrow narrow, about one sixth as long (sag.) as preglabellar area. Anterior border relatively long, it slopes gently upwards and forwards from the more steeply inclined anterior side of preglabellar furrow. Hypostome with moderately inflated, subcircular projection on anterior lobe of median body.

DESCRIPTION. Glabella longer than wide, outline sub-trapezoidal to bell-shaped, is not longer than fixed cheeks and protrudes moderately above them in lateral profile. Occipital ring fractionally wider than glabella, slightly convex (sag.) and longest medially, narrows abaxially, inflated into small node at axial furrow. Occipital furrow deepest and narrowest behind lateral glabellar lobe 1p. Lobe 1p has anterolateral abaxial corner more sharply angled than posterolateral, is partly divorced from central glabellar lobe by very shallow furrow connecting furrow 1p with occipital furrow.

Furrow 1p deep near axial furrow, runs inwards and moderately backwards then bifurcates; posterior branch trends more backwards, finally turning inwards more at right angles to median line; anterior branch trends forwards and inwards to meet posterior continuation of furrow 2p. Small inflation independant of central glabellar area within fork of furrow 1p. Lobe 2p joined to genal buttress. Elongate (tr.) lobe 3p defined anteriorly by short (tr.), sharp furrow 3p. Frontal lobe has bluntly rounded outline, falls steeply to preglabellar furrow.

Axial furrow deep and fairly narrow around lobe 1p, runs under lobe 2p and genal buttress, is widest opposite (tr.) lobe 3p and frontal lobe. Anterior pit positioned anterior to furrow 3p. Preglabellar furrow is moderately deep and narrow (sag.), expands (exs.) at antero-lateral corner of frontal lobe, narrows again and is continued, forwards and outwards between fixed cheek and anterior border into deep lateral border furrow; steeply sloping anterior side of preglabellar furrow meets anterior border at marked change of slope. Anterior border about one quarter (LM 2850) to about three tenths (holotype) as long as glabella, dorsal surface is very gently convex (sag.), sloping forwards and slightly upwards to moderately arched (tr.) anterior margin. In lateral profile the latter rises above anterior part of frontal lobe. Outer part of anterior border slopes downwards and backwards to rostral suture.

Morphology of fixed cheek and course of facial suture as in T. nodulosa. Width between palpebral lobes at least twice as wide as across glabella at lateral glabellar lobes 2p; mid-point of palpebral lobe opposite anterior part or margin of lobe 2p; length (exs.) of palpebral lobe about equal to lobe 2p. Narrow eye socle on free cheek. Inner part of free cheek slopes steeply to U-shaped lateral border furrow; junction of border furrow with lateral border is more angular (tr.) than with inner part of cheek. Lateral border rolled under ventrally.

Rostral suture and border sector of rostral plate imperfectly preserved but similar to T. nodulosa as far as can be determined (Pl. 1, fig. 8). Hypostome has sub-circular inflation on anterior lobe of median body. Oval macula smooth; median furrow very faint. Posterior border expanded into two posterior spines (Pl. 2, fig. 6).

Isolated and fragmentary thoracic segments (not figured) have axial rings inflated near axial furrow. Axis of pygidium only gently convex (tr.), has at least seven axial rings plus terminal axial piece. Each axial ring is widest and each ring furrow shallowest medially. Outer part of posterior axial rings bend slightly backwards. Seventh ring furrow does not reach axial furrow; very faint trace of eighth furrow confined to central part of terminal axial piece (Pl. 1, fig. 9, Pl. 2, fig. 7). Inner part of pleural region gently convex, outer part bent downwards more strongly to lateral margin. Five pleural furrows, best marked in their inner half, divide a wider anterior from narrower posterior pleural band. Interpleural furrows much weaker than pleurals.

Glabella, outer part of fixed cheek and free cheek have numerous small to medium-sized tubercles. Inner part of fixed cheek (especially anteriorly), genal buttress and anterior border have much larger tubercles, many of which are perforate. Deepest parts of glabellar and preglabellar furrows lack tubercles; lateral and posterior border furrows have scattered tubercles. Pygidial ornament, as far as can be determined, similar to outer part of fixed cheek.

DISCUSSION. Some variation is present in the anterolateral corners of the frontal lobe, depth of preglabellar furrow and length of anterior border to glabella. Compared to the holotype a specimen from outside the type area (LM 2850, Pl. 2, figs. 1, 3) shows these characters to be respectively more rounded in outline, less deep, and relatively shorter. As specimens from Dolyhir are seen to vary in a like-manner (for example GSM Zs58, Pl. 1, figs. 6-8, Pl. 2, fig. 10, in the first two of these characters), the variation is within that here allowed to this species and not sufficient to serve as a basis for further separation.

T. volsoriforma differs from T. vulpecula most obviously by its much shorter preglabellar furrow, longer anterior border, and narrower (tr.) axial furrow anterior to lateral glabellar lobe 2p. The hypostome of volsoriforma has an inflated raised area on the anterior lobe which seems different to the well developed projections present in T. vulpecula and T. nodulosa, though this distinction must be confirmed by better preserved material of volsoriforma. If this difference can be more firmly established, it suggests a more conspicuous projection was developed later in the phyletic series.

OCCURRENCE. Only recorded in situ from the type stratum of the type area, but one water-transported specimen (LM 2850) was collected from a stream bed near English bridge, Shrewsbury. The species may therefore have had a greater geographical and stratigraphical range than lowermost Wenlock Series of the Old Radnor Inlier.

Tapinocalymene cf. T. volsoriforma sp. nov.

Plate 2, figs. 8, 11.

MATERIAL. Two individuals - one, a distorted, incomplete external mould of a cephalon plus its counterpart, DJS/89 a-b, the other, a poorly preserved internal mould of an incomplete cranidium, DJS/90. Collected by Mr. C.N. Rodgers, University of Birmingham.

OCCURRENCE. Wenlock Shale, cutting on the north side of a bend in the A489 road between Horderley and Plowden, southern side of the Long Mynd, Shropshire (Nat. Grid. Ref. SO 402875). Graptolites collected from this locality are not sufficient to provide an exact Zone for the horizon but are identified by Dr. I. Strachan, University of Birmingham as M. flemingii of "post riccartonensis Zone" age (pers. comm. with Mr. C.N. Rodgers).

DISCUSSION. The glabellar ornamentation of this species, as seen on a cast of an external mould, clearly identifies it with members of Tapinocalymene gen. nov. In particular the long (sag.) anterior border puts it closest to T. volsoriforma, but a more definite determination is precluded by the effects of crushing and distortion. The significance of these specimens lies in the possibility that T. volsoriforma, or a species close to it, existed outside the type area at a later date.

Tapinocalymene vulpecula sp. nov.

Plate 3; Text-figs. 1G-H.

DERIVATION OF THE NAME. Latin, diminutive of vulpes, fox, alluding to the appearance of the hypostome when viewed with the posterior spines in an anterior position, suggesting a fox's head.

HOLOTYPE. An incomplete cranidium; DJS/48, collected Derek J. Siveter 1971; Pl. 3, figs. 1, 2, 12.

TYPE STRATUM AND TYPE LOCALITY. Wenlock Shale, small disused quarry on the western side of the road from Letton to Walford, a quarter of a mile north of Letton, near the Wigmore Rolls area, Welsh Borderland (Nat. Grid. Ref. SO 3790 7080). Graptolites (SM A84000-009, SM A80387-391) collected from this locality have been assigned by Dr. R.B. Rickards, Sedgwick Museum, Cambridge, to M. flemingii (Salter), and "probably belong to the lundgreni Zone"(pers. comm.).

ADDITIONAL MATERIAL. Three incomplete cranidia, DJS/75-77; two pygidia, one almost complete with exoskeleton remaining, DJS/79, the other a complete internal mould, DJS/80; one incomplete internal mould of a hypostome and its counterpart, DJS/78. Numerous other fragmentary cranidia, pygidia and thoracic segments.

DIAGNOSIS. Preglabellar area about two fifths as long as glabella. Preglabellar furrow about as long (sag.) as anterior border and half as long as preglabellar area. Marked break in slope where anterior side of furrow meets posterior margin of border.

DESCRIPTION. Glabella shorter than fixed cheek, slightly longer than wide. Occipital ring gently convex and widest at median line, narrows abaxially and is mildly inflated near axial furrow. Occipital furrow widest and transversely directed across posterior part of central glabellar lobe, becomes deeper swinging backwards behind lateral glabellar lobe 1p. Lateral lobe 1p is about one-third as wide as glabella. Lateral glabellar furrow 1p deep and narrow between lobes 1p and 2p, then bifurcates into posterior and slightly shorter anterior branch. Posterior branch continues further inwards and more backwards before dying out; shallow, broad (trans.) depression connects this branch to occipital furrow. Anterior branch runs forwards and inwards around lobe 2p. Small intermediate lobe present between these branches. Lateral lobe 2p connected to adaxially projecting genal buttress. Small lobe 3p perched on dorsolateral surface of glabella, bounded anteriorly by short (tr.) furrow 3p. Frontal lobe has well rounded anterolateral corners and slightly convex forwards anterior margin which falls vertically to preglabellar furrow.

Axial furrow at least twice as wide at lobe 3p and frontal lobe than around furrow 1p. Anterior pit situated in axial furrow below lateral glabellar furrow 3p. Preglabellar furrow deep, U-shaped (sag.), about as long as anterior border but shortens (exs.) abaxially where fixed cheek approaches anterior border; anterior side of furrow is about vertical and meets posterior part of anterior border in a sharp break of slope, border then continues forwards and upwards at less steep angle until swinging over ventrally at anterior margin to slope to rostral suture (Pl. 3, fig. 2). Anterior border of about constant length abaxially from median line until opposite (exs.) axial furrow, thereafter narrowing towards facial suture. In lateral profile anterior margin is about level with or just above height of frontal lobe; in dorsal view it is gently arched forwards.

From palpebral lobe fixed cheek is more dorsally convex and slopes (exs.) more steeply to abaxial continuation of preglabellar furrow than to posterior border furrow. Inner, anterior corner of fixed cheek well rounded in dorsal view. Mid-point of palpebral lobe lies opposite anterior part of 2p lobe. Posterior branch of facial suture runs outwards from palpebral lobe, then sweeps backwards towards lateral border furrow, course thereafter unknown. Anterior branch is abaxially convex, runs forwards and inwards to anterior margin.

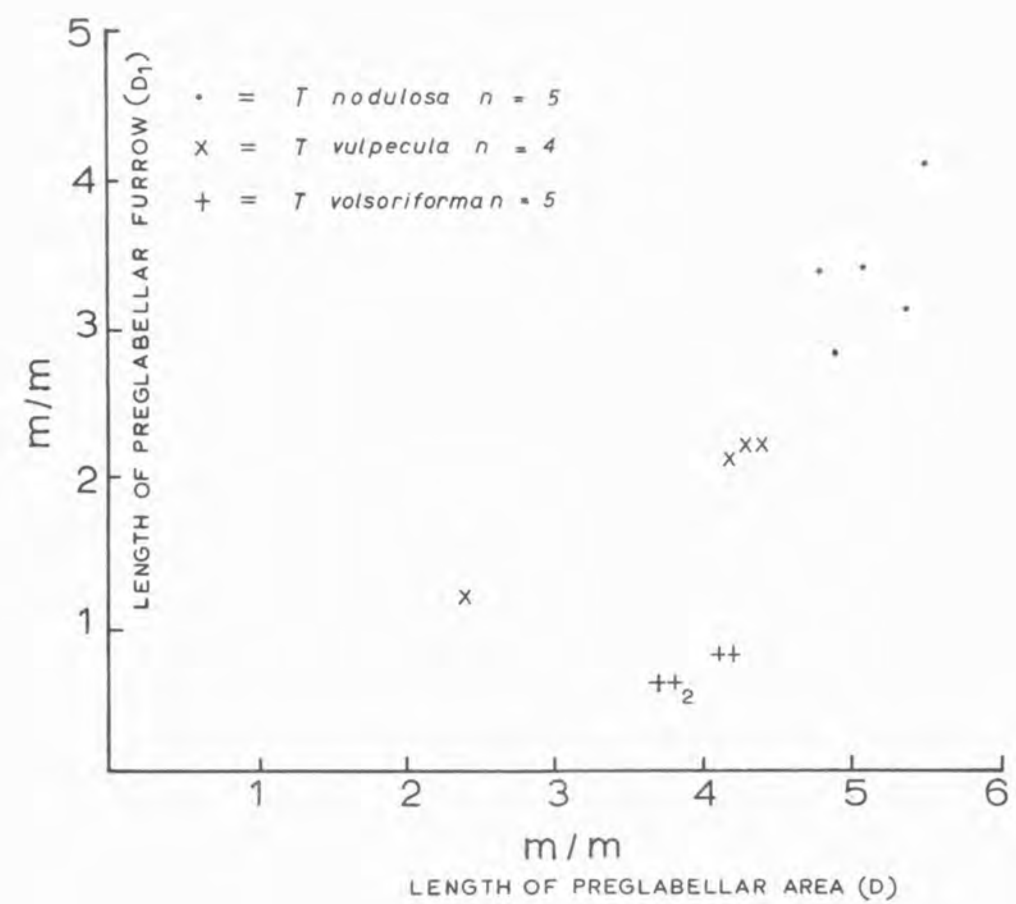
Rostral plate unknown. Anterior border of hypostome sharply flexed ventrally; anterior border furrow weakly defined. Deep pit in large anterior wing. Between anterior and posterior wings lateral margin is embayed but also slightly convex abaxially. Lateral border convex (tr.), narrows towards posterior wing; lateral border furrow deepest opposite (tr.) middle of anterior lobe, shallowest opposite macula, wider and moderately deep at posterior wing. Posterior border flattened, extended into two long, pointed spines; posterior border furrow short (tr.) and sharply incised at junction of two spines. Median body divided into two unequal (sag.) lobes by median furrow. The latter is best marked at, and runs from anterior part of lateral border furrow to swollen, oval-shaped macula; its posteriorly convex course between maculae is indistinct. Anterior lobe bears prominent, anteroventrally directed median projection; in profile (sag.) anterior side of this lobe is concave upwards, posterior side is gently convex. Posterior lobe of median body is crescent-shaped. (Pl. 3, figs. 3, 11).

Pygidial axis has six complete, one incomplete axial rings; each ring very gently convex (tr. & sag.). Anterior six ring furrows shallowest at central one-third of their length (tr.), deepen quickly in outer one-third to axial furrow; very faint seventh ring furrow does not reach axial furrow. The latter is weakest around terminal axial piece. Inner pleural region slopes very gently to cincture, thereafter more steeply to lateral margin. Five pleural furrows run outwards and backwards to cincture, apparently absent from here to lateral margin though this part of pygidium is imperfectly preserved. Interpleural furrows extremely faint, best seen near axial furrow, not marked on internal mould (compare Pl. 3, fig. 4 with Pl. 3, fig. 5).

Cranidial tubercles not well preserved, but of same pattern as T. nodulosa and T. volsoriforma. Whole ventral surface of hypostome covered with small pustules increasing in density on lateral borders; maculae almost completely non-pustulate. Small to medium sized tubercles scattered all over pygidium except deepest part of axial, ring, and pleural furrows.

DISCUSSION. The differences of T. vulpecula from T. nodulosa and T. volsoriforma are given under the discussions of those species.

OCCURRENCE. Known only from the type stratum and type locality.



5
4
3
2
1
m/m
LENGTH OF PREGLABELLAR FURROW (D1)
• = T nodulosa n = 5
x = T vulpecula n = 4
+ = T volsoriforma n = 5
2
1
2
3
4
5
6
m/m
LENGTH OF PREGLABELLAR AREA (D)

TEXT-fig.12

Tapinocalymene nodulosa (Shirley, 1933)

Plates 4-7; Text-figs. 1A-F

1839 Calymene Blumenbachii Brongniart; Murchison (pars), p. 653, pl. 7, fig. 5 (GSM 6588), non figs. 6, 7.

1848 Calymene tuberculosa, Salter; Salter, p. 342, pl. 7, figs. 1, 1a (GSM 19642), 2, 3, 5, ? fig. 4.

1849 Calymene tuberculosa Salter; Salter, p. 1, pl. 8, figs. 1, 2 (GSM 19642), 3-5, 7, ? fig. 6, non figs. 8, 8* (GSM 19690).

non 1851 Calymene tuberculosa (Salt.); McCoy in Sedgwick & McCoy, p. 167.

1854 Calymene tuberculosa, Salter; Murchison, pl. 18, fig. 11.

1865 Calymene tuberculosa, Salter; Salter, p. 91, pl. 8, figs. 1, 2 & 3 (GSM 19642), 4, 5 (GSM 19646), 6.

1873 Calymene tuberculosa, Salter; Salter (pars), p. 133.

non 1873 Calymene tuberculosa, Salter; Salter, p. 166.

1885 Calymene tuberculosa of Salter; Lindström, p. 66.

1918 Calymene Blumenbachii Brongniart; Reed? in Garwood & Goodyear, p. 20.

1925 Calymene tuberculosa SALT.; Warburg, p. 158.

1927 Calymene (Diacalymene) tuberculosa Salter; Kegel, pp. 618, 620, text-fig. 2f.

1933 Calymene nodulosa nom. nov.; Shirley, p. 53, pl. 1, figs. 6-11,

1936 Calymene nodulosa Shirley; Shirley, pp. 388, 390, 393, 399, 400, text-fig. 1. (pars), text-fig. 2. (pars).

? 1953 Calymene nodulosa Shirley; Williams, pp. 199, 200.

1970 Calymene nodulosa Shirley, 1933; Schrank, pp. 115, 122, 123.

1970 Spathacalymene nodulosa (Shirley); Tomczykowa, pp. 63, 70, 72, text-figs. 4k, 5f.

1971 Calymene nodulosa Shirley 1933; Whittington, p. 463.

HOLOTYPE. A nearly complete individual (minus its preglabellar area), with the cuticle removed from the abaxial part of the cheeks and pleural region of the thorax; GSM 19642; figured Salter 1848, pl. 7, figs. 1, 1a and 1849 pl. 8, figs. 1, 2, also Shirley 1933, pl. 1, figs. 6 - 10, also herein Pl. 5, figs. 1 - 3.

TYPE STRATUM AND TYPE LOCALITY. Wenlock Shale, Burrington, Herefordshire. The exact locality at Burrington where the holotype came from is unknown and a recent study of the graptolites (Holland, Rickards & Warren, 1969, p. 677, text-fig. 4) has shown that outcrops of Wenlock Shale in the Burrington district fall within both the C. lundgreni and M. ludensis Zones. The laneside exposure 460 yards NNE of Burrington Church (locality 61 of Holland, Lawson and Walmsley 1963, pp. 132, 136, 163) lies within the ludensis zone; exposures in the sides of the sunken lanes, 230 yards S of the church (locality 91 of Holland et al. 1963, p. 164) belong to the lundgreni Zone. I have collected this species from the latter locality but the possibility cannot be dismissed that extant museum specimens, including the holotype, have been obtained from ludensis Zone strata.

ADDITIONAL MATERIAL. More than fifteen incomplete cranidia and pygidia, several (more than 6) nearly complete individuals. Five hypostomes. There is material of this species in the British Museum, Geological Survey Museum, National Museum of Wales, Hunterian Museum, and Ludlow Museum.

DIAGNOSIS. Preglabellar area is from about two fifths to one half as long as glabella, is directed forwards and progressively more steeply upwards. Preglabellar furrow about three fifths to three quarters as long as preglabellar area; transition between steep anterior side of this furrow and narrow (sag. & exs.) anterior border characterized by gradual break in slope. Hypostome with prominent median node on anterior lobe and conspicuous ovate maculae.

DESCRIPTION. Cranidium about twice as wide as long (sag.). Glabella is longer than wide, with a trapezium-like to bell-shaped outline; in lateral profile its dorsal surface is above fixed cheek at lateral glabellar lobe 1p, though is equal to or can assume a height below fixed cheek at about lateral glabellar furrow 2p (Pl. 4, fig. 6). Occipital ring about one quarter as long (sag.) as wide, just greater than one quarter as long as and slightly wider than glabella; it is longest medially then narrows and swings forwards laterally towards posterolateral corner of 1p lobe where it is swollen into a node. Occipital furrow widest and shallowest medially, narrows and deepens abaxially towards axial furrow, has a more steeply inclined posterior than anterior slope (sag.). Lateral glabellar lobe 1p about one third as wide as glabella. Abaxial part of 1p furrow deep, divides adaxially into two branches; posterior branch runs inwards and obliquely backwards, shallows before turning finally towards median line; weaker anterior branch directed forward and inward, not reaching as far adaxially as posterior branch. Shallow extension of posterior branch connects with occipital furrow to separate 1p lobe from frontomedian lobe. Small, but definite supplementary lobe lies within fork of furrow 1p. Lateral lobe 2p is papillate, joined to adaxially directed genal buttress. Lateral furrow 2p directed inward and slightly backward, is continued as sharply flexed shallow depression which meets anterior branch of furrow 1p, thus semi-isolating lobe 2p. Lateral lobe 3p much smaller than 2p, slightly elongated (tr.), sited on dorsolateral glabellar surface. Furrow 3p directed at about right angles to median line. Possible 4p furrow, which is not observed dorsally, is expressed ventrally as a ridge joined to outer, posterior end of ridge which represents furrow 3p (Pl. 7, figs. 2, 8). Frontal lobe bluntly rounded in outline, falls steeply to preglabellar furrow.

Axial furrow deep, steep-sided and most narrow around lobe 1p, shallows running under bridge of lobe 2p and genal buttress, widens (tr.) greatly anterior to this, fanning out markedly on reaching preglabellar furrow. Anterior pit is deep, situated very low down on adaxial side of axial furrow just anterior to furrow 3p. Anterior pit represented ventrally by a boss, the inner anterior slope of which is hollowed for reception of anterior wing process of hypostome (Pl. 7, figs. 2, 8). Some specimens show vestige of eye ridge running down abaxial side and across (tr.) base of axial furrow opposite lateral furrow 3p (Pl. 6, fig. 3, Pl. 7, fig. 4). In dorsal view anterior margin of preglabellar area is moderately to strongly convex forwards, in lateral profile it is raised fractionally above frontal glabellar lobe, in frontal view it is sometimes slightly swollen upwards opposite axial furrow (Pl. 6, fig. 8). Long (sag. & exs.) preglabellar furrow passes smoothly forwards and progressively more upwards on its anterior slope into short, convex upwards (sag.) anterior border. Outer part of anterior border slopes downwards and slightly backwards to rostral suture.

Posterior border of cranidium marginally increases width (exs.) from axial furrow to fulcrum abaxially from which it expands more quickly until narrowing slightly near facial suture; convexity (exs.) of border decreases towards facial suture. Posterior border furrow widest at about mid-length, has a less steeply inclined anterior than posterior slope, both slopes become more gently inclined abaxially. Postocular part of fixed cheek slopes moderately downwards to border furrow; preocular part projects beyond frontal lobe, is vertical or slightly overhangs abaxial continuation of preglabellar furrow. Mid-point of palpebral lobe is opposite lateral lobe 2p, initially it continues slope of fixed cheek then abaxially has a more horizontal attitude. Posterior branch of facial suture runs firstly outwards and slightly backwards before swinging in broad curve to lateral border and finally turning sharply posteriorly to meet posterior margin;

anterior branches are abaxially convex, slightly convergent. Free cheek slopes steeply to U-shaped lateral border furrow. Doublure of free cheek sharply reflexed upwards and outwards from lateral border.

Rostral plate composed of outer border sector and inner doublure sector; border sector from two fifths to one half as long (sag.) as wide, about three times as long as outer part of anterior border. Rostral suture moderately arched, abaxially it is slightly convergent towards anterior margin of cranidium. Connective sutures gently convex outwards, converge posteriorly towards angular junction of border and doublure sectors. Inner arc of border sector about parallel to rostral suture, marked by a slight ridge, is wider than embayment of anterior margin of hypostome (Pl. 7, fig. 3). Hypostome is wider across its anterior wings than long (sag.). In ventral view anterior margin is broadly convex forwards. Anterior border is flexed ventrally; anterior border furrow shallow and narrowest medially, becoming wider laterally near deep pit of anterior wing. Lateral margin slightly convex abaxially between anterior and posterior wings; lateral border narrows (tr.) posteriorly; lateral border furrow deepest opposite (tr.) spur of anterior lobe. Posterior border flattened, projecting into two spines. Faint, convex backwards median furrow connects two conspicuous, ovate maculae. Anterior lobe of median body about two and a quarter to two and a half times as long as posterior lobe; a hook-like projection is directed anteroventrally from centre of anterior lobe. Posterior lobe is crescent-shaped.

Thorax characteristically broad (tr.); anterior part of axis less wide than pleural region. Axis has 13 rings, each is of about constant width (sag. & exs.), flat to gently convex in lateral profile, flexed forwards abaxially and swollen into a node at axial furrow. Posterior band of each pleuron higher than anterior, moderately convex (exs.), forms posterior rim to articulating facet. Pleural furrow moderately deep and U-shaped at fulcrum, becomes less well marked abaxially, dying out on articulating facet. Many specimens show a kink in the distal, posterior margins of thoracic pleurae; it is most obvious and more dorsally positioned on posterior pleurae, becomes successively lower on anterior pleurae, and is continued posteriorly as a cincture on the pygidium (Pl. 4, figs. 3, 5, 6; Pl. 5, figs. 4-6).

Pygidium about two and a half times as wide as long. Axis is at most very gently convex (tr.) and much less arched than thorax, contains six distinct and one indistinct axial rings and terminal axial piece. Each ring is almost flat (sag.); anterior rings slightly inflated at axial furrow though not flexed forwards as in thorax. Ring furrows shallowest medially, become deeper towards axial furrow. Latter is best marked anteriorly, becomes weaker posteriorly, scarcely present around terminal axial piece. Inner pleural region slopes gently (tr.) to cincture, thereafter much more steeply to lateral margin. Pleural region normally has five distinct pleural furrows to the cincture, abaxially from which they fade markedly; one specimen (Pl. 5, figs. 7, 9, 10) has trace of a sixth pleural furrow. Interpleural furrows faint. Postaxial sector falls almost vertically from terminal axial piece.

Small to medium sized tubercles are evenly distributed on glabella; much larger ones present on genal buttress, anterior adaxial part of fixed cheek, and sometimes anterior border. Preglabellar and axial furrows lack tubercles. Abaxial nodes of occipital and axial rings have concentration of about 30 to 50 tubercles. Medium sized, closely spaced tubercles on border sector of rostral plate and lateral border of cheek. Scattered tubercles found on hypostome, thorax and pygidium. Hypostomal maculae and deepest part of furrows (pleural, axial, articulating) lack ornamentation. Many tubercles are preforate, canals connect these openings to ventral side of exoskeleton.

DISCUSSION. Recent collecting has provided much new information on this species. It is unfortunate that the holotype does not have its preglabellar area present, as this is important for specific discrimination within the genus, but specimens used by Shirley in his description (GSM 19644, GSM 19646), and others from Burrington, display this character well. Variation is present in the amount of upcurving of the preglabellar area and the degree of impression of cincture and interpleural furrows on the pygidium, though the latter are never very strongly developed and may be almost completely absent. The largest cranidium examined (Pl. 4, fig. 7, Pl. 5, fig. 8) is the only specimen to have a glabella about equal in length with the fixed cheek.

Some cranidia from calcareous concretions within the Wenlock Shale at Dolyhir (see GSM 195, Pl. 6, figs. 1, 4, 7) are most interesting because their anterior border is more swollen, and preglabellar furrow thus relatively shorter, than in typical specimens from Burrington. They therefore approach _T. vulpecula_ sp. nov., but are regarded closer to _T. nodulosa_ because they lack the more distinct, sudden break in slope between preglabellar furrow and anterior border that is diagnostic of the new species. The cranidia with the more swollen border may represent a separate subspecies of _nodulosa_, but the anterior border of other specimens from Dolyhir is very similar to that in Burrington material, and prevents constant discrimination of this character between the two allopatric populations (compare Pl. 6, figs. 6, 10, 11, with Pl. 4, figs. 1, 3, 5, 6). I have tried to separate the taxa at useable, distinct morphological discontinuities and refrain from over-splitting the genus.

T. nodulosa is distinguished from _T. volsoriforma_ and _T. vulpecula_ by a longer preglabellar furrow and shorter anterior border, together with the more gradual transition in slope between these two features (compare diagnoses). It also has a longer preglabellar area relative to glabellar length than in _volsoriforma_ (from about two fifths to one half and about one third respectively), though there is some degree of coincidence in this proportion between nodulosa and vulpecula (about two fifths in some specimens of both species). During the evolutionary series from T. volsoriforma to T. nodulosa the inflation between the adaxial fork of lateral furrow 1p appears to become stronger, and the axial furrow anterior to lateral lobe 2p wider (tr.).

OCCURRENCE. In addition to the type locality Shirley (1933, p. 56) recorded the species from a quarry at the side of Nant Tresglen, behind "Half-Way-Inn", five miles east of Llandovery (Nat. Grid. Ref. SN 828 328). These specimens were found by S.H. Straw and associated with a fauna of Wenlock age; they have not been examined as their repository is unknown to me and an attempt at re-collection has proved fruitless.

Williams (1953, pp.199, 200) records C. nodulosa from his "Lower" and "Upper" Wenlock groups of the Llandeilo district; N.H. Kirk (unpublished part of Ph.D. thesis) lists the species from the "Wenlock Mudstones" near Upper Hanter Farm, SSE of Dolyhir, and a quarry NW of the Folly, S of Presteigne, Radnorshire. The specimens which formed the basis for these recordings have not been examined. At the nearby Nash Scar Quarry, near Presteigne, the Wenlock Shale above the faulted contact with the Nash Scar Limestone is of lundgreni Zone age (Bassett 1972, p. 54). Cocks et al. (1971, p. 109, fig. 2) record the 'Wenlock Shales' of the Presteigne area as ranging from the top part of the riccartonensis Zone to the base of the lundgreni Zone. They are followed by the 'Olive Mudstones'.

A small area of Wenlock Shale on top of the Dolyhir Limestone at the south side of Garwood and Goodyear's (1918, p. 20, pl. 5, fig. 1) quarry 'D', Dolyhir, Radnorshire, has yielded the beautifully preserved specimens referred to in the discussion. As far as I am aware the zone(s) represented by the Wenlock Shale of this quarry is unknown.

The writer has collected this species from the Wenlock Shale of Birtley Lane, four miles SSW of Leintwardine, Wigmore Rolls area, Welsh Borderlands (DJS/86-7, Nat. Grid. Ref. SO 3687 6888), and the Coalbrookdale Beds (probably lundgreni Zone) near the beginning of the track section behind Eaton Church, Apedale, Shropshire (Nat. Grid. Ref. SO 5001 9002). The Geological Survey have recorded it from the Wenlock Shale near Rushbury, Apedale (Greig, Wright et al. 1968, pp. 340, 353, 354). An isolated pygidium of Tapinocalymene (DJS/91, not figured) from the transition between the Coalbrookdale Beds and Tickwood Beds behind Eaton Church (Nat. Grid. Ref. SO 50239002), may also belong to nodulosa.

Subfamily FLEXICALYMENINAE sub. fam. nov. (herein)

Genus PALACALYMENE gen.nov.

DERIVATION OF THE NAME. From the latin, Pala, shovel, alluding to the form of the preglabellar area.

TYPE SPECIES. Spathacalymene flexuosa Tomczykowa, 1970, p. 80 pl. 2, figs. 5a-c; from the Upper Mielnik Beds, Saetograptus leintwardinensis Zone, Ludlow Series, at a depth of 940.5 m in the Mielnik borehole, Mielnik, Poland.

OTHER SPECIES. P. brevis (Tomczykowa, 1970), P. linguata (Tomczykowa, 1970), P. ? pompeckji (Kummerow, 1928).

DIAGNOSIS. Preglabellar area is long - from about one third to two-thirds as long as the glabella, it is narrow (tr.), U-shaped to V-shaped in outline, projects forwards and is variably inclined upwards. Glabella is bell-shaped in outline; frontal lobe very rarely projects in front of fixed cheek. In lateral profile dorsal surface of fixed cheek is equal to or rises slightly above surface of glabella. Cranidium lacks genal buttress. Rostral plate is long (sag.). Pygidium has deep relatively short pleural furrows, fairly wide smooth border, and extremely weak or no interpleural furrows.

DISCUSSION. Four of the species included by Tomczykowa (1970) in Spathacalymene Tillman, 1960 are here removed from that genus as, amongst other things, they lack the papillate-buttress structure on the cranidium; three of these species (S. brevis, S. linguata, S. flexuosa) are considered to belong to a new taxon, Palacalymene, and the fourth (Calymene pompeckji Kummerow, 1928) is questionably referred to this genus which is placed in the Flexicalymeninae subfam. nov. (herein). A similar course of action with respect to the three Polish species was anticipated by Whittington (1971, pp. 457-59). The combination of features given in the above diagnosis serves to distinguish Palacalymene from all other genera within the Flexicalymeninae (for example Flexicalymene, Gravicalymene, Thelecalymene). Other genera of this subfamily, as here conceived have not been recorded from the Polish Silurian, but they are known from strata of this age elsewhere (Whittington,1971; Shirley, 1938; Haas, 1968; Chatterton, 1971; Alberti, 1969).

Palacalymene and Tapinocalymene are thought to belong to two separate major evolutionary stocks, but it is of interest to note that both genera have several characters in common. These include the height and length of the glabella to the fixed cheek, widely separated, palpebral lobes (measurements taken from Tomczykowa's plates indicate from about two and a quarter to two and a half times as wide as lateral lobes 2p), a very weakly convex (tr.) pygidial axis, faint interpleural furrows and a cincture on the outer pleural region of the pygidium. Moreover in some specimens of linguata the cranidial tubercles appear to become coarser on the anterior part of the fixed cheek as in Tapinocalymene (see Tomczykowa 1970, pl. 4, fig. 9a; pl. 5, fig. 9a). However most specimens of Palacalymene show fairly coarse tubercles on both the glabella and the fixed cheek and also on the preglabellar area (see Tomczykowa 1970, pl. 2, fig. 7a), and this is quite unlike the ornamentation in members of Tapinocalymene. A further difference between the two genera is the much more steeply descending frontal glabellar lobe in species of the British genus. It would be interesting to know the form of the hypostome in Palacalymene. Tomczykowa (1970, p. 80) refers to a fragmentary hypostome of P. flexuosa but it does not seem to have been described or figured. Calymenids exhibiting the papillate-buttress structure all (calymenines) show a more or less marked protruberance on the anterior lobe of the median body.

OCCURRENCE. Ludlovian of Poland; possibly from the Graptolithengestein (Wenlock - upper Ludlow) erratics of Neubrandenburg, N German Plain.

The descriptions and occurrences of P. brevis, P. linguata and P. flexuosa are adequately dealt with by Tomczykowa and are not repeated here, though for convenience I have included data on the type specimens. It was Tomczykowa's belief that all these species lacked interpleural furrows but at least P. linguata, pl. 3, figs. 9a, 10a and P. flexuosa, pl. 5, fig. 5a) show very weak signs of them.

Palacalymene brevis (Tomczykowa, 1970)

Not figured

1970 Spathacalymene brevis n. sp.; Tomczykowa, p. 82, pl. 1, figs. 1-7, pl. 2, fig. 4, pl. 3, figs. 1, 4-8, pl. 5, figs. 1-4, text-figs. 4a-c, 5g.

HOLOTYPE. An incomplete cranidium; IG. 1169.II.52; figured by Tomczykowa 1970, pl. 1, figs. 7a-c, text-fig. 4a.

TYPE STRATUM AND TYPE LOCALITY. Silurian, Ludlow Series, Upper Mielnik Beds, Saetograptus leintwardinensis Zone, at a depth of 1203.6 m in the Goldap borehole, Goldap, Poland.

REMARKS. Differs from P. linguata and P. flexuosa mainly because of its shorter, slightly more V-shaped proboscis. It is suspiciously like P.? pompeckji (Kummerow, 1928).

Palacalymene linguata (Tomczykowa, 1970)

Not figured

1970 Spathacalymene linguata n. sp.; Tomczykowa, p. 77, pl. 3, figs. 9, 10, pl. 4, figs. 1-4, 6-9, pl. 5, figs. 6, 7, 9-12, text-figs. 4g-i, 5i

HOLOTYPE. An incomplete cephalon, lacking the right fixed cheek; IG.1169.II.5; figured by Tomczykowa 1970, pl. 4, figs. 9a-d, text-fig. 4g.

TYPE STRATUM AND TYPE LOCALITY. Silurian, Ludlow Series, Upper Mielnik Beds, Cucullograptus hemiaversus Zone, at a depth of 959.1 m in the Mielnik borehole, Mielnik, Poland.

REMARKS. This species has the longest proboscis; it can reach up to two-thirds as long as the glabella.

Palacalymene flexuosa (Tomczykowa, 1970)

Not figured

1970 Spathacalymene flexuosa n. sp.; Tomczykowa, p. 80, pl. 1, figs. 8, 9, pl. 2, figs. 1-3, 5-7, pl. 3, figs. 2-3, 11-16, pl. 4, fig. 5, pl. 5, figs. 5, 8, text-figs. 4d-f, 5e.

HOLOTYPE. A cranidium; IG.1169.II.7; figured by Tomczykowa 1970, pl. 2, figs. 5a-c, text-fig. 4d.

TYPE STRATUM AND TYPE LOCALITY. Silurian, Ludlow Series, Upper Mielnik Beds. Saetograptus leintwardinensis Zone, at a depth of 940.5 m in the Mielnik borehole, Mielnik, Poland.

REMARKS. Differs from both P. brevis and P. linguata mainly in the strong, upwards curve of its proboscis - which can be almost vertically inclined.

Palacalymene pompeckji (Kummerow, 1928)

Not figured

1928 Calymmene Pompeckji n. sp.; Kummerow, p. 9, pl. 1, figs. 5a, b.

1970 Calymene pompeckji KUMMEROW, 1928; Schrank, p. 120, pl. 1, fig. 5, non figs. 4, 6, non pl. 2, figs. 1-3, 7.

1970 Spathacalymene pompeckji, Kummerow, 1928; Tomczykowa, p. 70, text-fig. 4f.

1971 Calymene pompeckji Kummerow 1928; Whittington (pars), p. 463.

HOLOTYPE. By monotypy; an almost complete individual; MB.1969.31; figured Kummerow 1928, pl. 1, figs. 5a, b, and Schrank 1970, pl. 1, fig. 5.

TYPE STRATUM AND TYPE LOCALITY. From the green-grey Graptolithengestein (Wenlock to the top of the Leintwardine Stage, Ludlow Series) erratics of Butzow, Bezirk Neubrandenburg, North Germany. Schrank (1970, p. 123) notes that the lithology of the matrix enclosing the holotype suggests that it comes from the Graptolithengestein, though Kummerow (1928, p. 9) originally stated from the stratigraphically later Beyrichienkalk.

ADDITIONAL MATERIAL. None known.

DISCUSSION. This species has recently been revised by Schrank (1970, p. 120). In his study Schrank observed that small cranidia of certain Calymene species are deficient in the papillate-buttress structure at lateral glabellar lobe 2p, but that it is gained later in ontogeny. The lack of this feature in the type (and only known) specimen of pompeckji was at first sight surprising, and Schrank recognised that it gave grounds for transference of the species to another genus, but he accounted for the absence of the structure by noting the juvenile stage of the holotype. He proceeded to regard pompeckji as a senior synonym of Calymene neointermedia R. & E. Richter, 1954, mainly because both have a relatively long, forward and upwardly projecting preglabellar area.

However an examination of topotype material of neointermedia (discussed by me elsewhere)has revealed that the axial furrow is bridged in specimens of this species well before they reach a size equivalent to that of the pompeckji holotype, and this together with other differences strongly suggests that these two species are not synonymous.

Furthermore two other Calymene taxa, C. tuberculosa Dalman, 1827 and C. lawsoni Shirley, 1962, also have the papillate-buttress structure already present prior to attaining the same size as the pompeckji holotype, which seriously puts into question the assignment of pompeckji to Calymene. Until the time of contact between genal buttress and lobe 2p is accurately documented in many more species of Calymene, and this shows a range of variation which includes pompeckji, I remain unconvinced that the holotype of the latter is a juvenile individual of a papillate-buttressed Calymene. At present a relationship closer to members of Ewacalymene seems more likely.

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A thesis entitled

TRILOBITES OF THE FAMILY CALYMENIDAE FROM THE ORDOVICIAN, SILURIAN AND DEVONIAN SYSTEMS OF NORTH-WEST EUROPE

Submitted for the degree of

DOCTOR OF PHILOSOPHY

in the

FACULTY OF SCIENCE

UNIVERSITY OF LEICESTER

by

DEREK JAMES SIVETER B.Sc.

Volume 2, plates

December, 1973

CHAPTER A   PLATES 1-13

THE CALYMENID GENUS *PHAROSTOMA* FROM THE ORDOVICIAN OF BRITAIN, SCANDINAVIA AND BOHEMIA.

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PLATE 1

Figs. 1-7. Pharostoma vokovicense Snajdr, 1956

1, 3, 5-7. Holotype, incomplete cephalon, 'Silcoset' rubber cast of external mould (fig. 1, 3, 5, 6) and plaster cast of internal mould (fig. 7), NMP 184/67, Sarka Formation (Llanvirn), brickyard under the Cerveny vrch hill, Vokovice, Prague district. Dorsal view, anterodorsal view, left oblique stereo-pair, left lateral view, dorsal view 1.8. Figured Snajdr 1956, pl. 5, fig. 1 (internal mould).

2, 4. Incomplete cranidium, internal mould, BM I5408, Sarka Formation, Rokycany, Czechoslovakia. Dorsal, right oblique views, x 3.

Figs. 8-11. Pharostoma pulchrum pulchrum (Beyrich, 1846)

8, 10, 11. Incomplete cephalon, plaster cast of internal mould, NMP It327 CD689, Letna Formation, Vesela ?, Czechoslovakia. Left oblique, dorsal, left lateral views, x 1½. Figured Barrande 1852, pl. 19, figs. 4, 5 (plate reversed) as Calymene pulchra Barr.

9. Incomplete cranidium, 'Silcoset' rubber cast of external mould, GSM 86861, topmost Hope Shales, lower Llanvirn, path W of Brithdir, near Old Church Stoke, Montgomeryshire. External mould of this specimen figured Whittard 1960, pl. 18, fig. 5.

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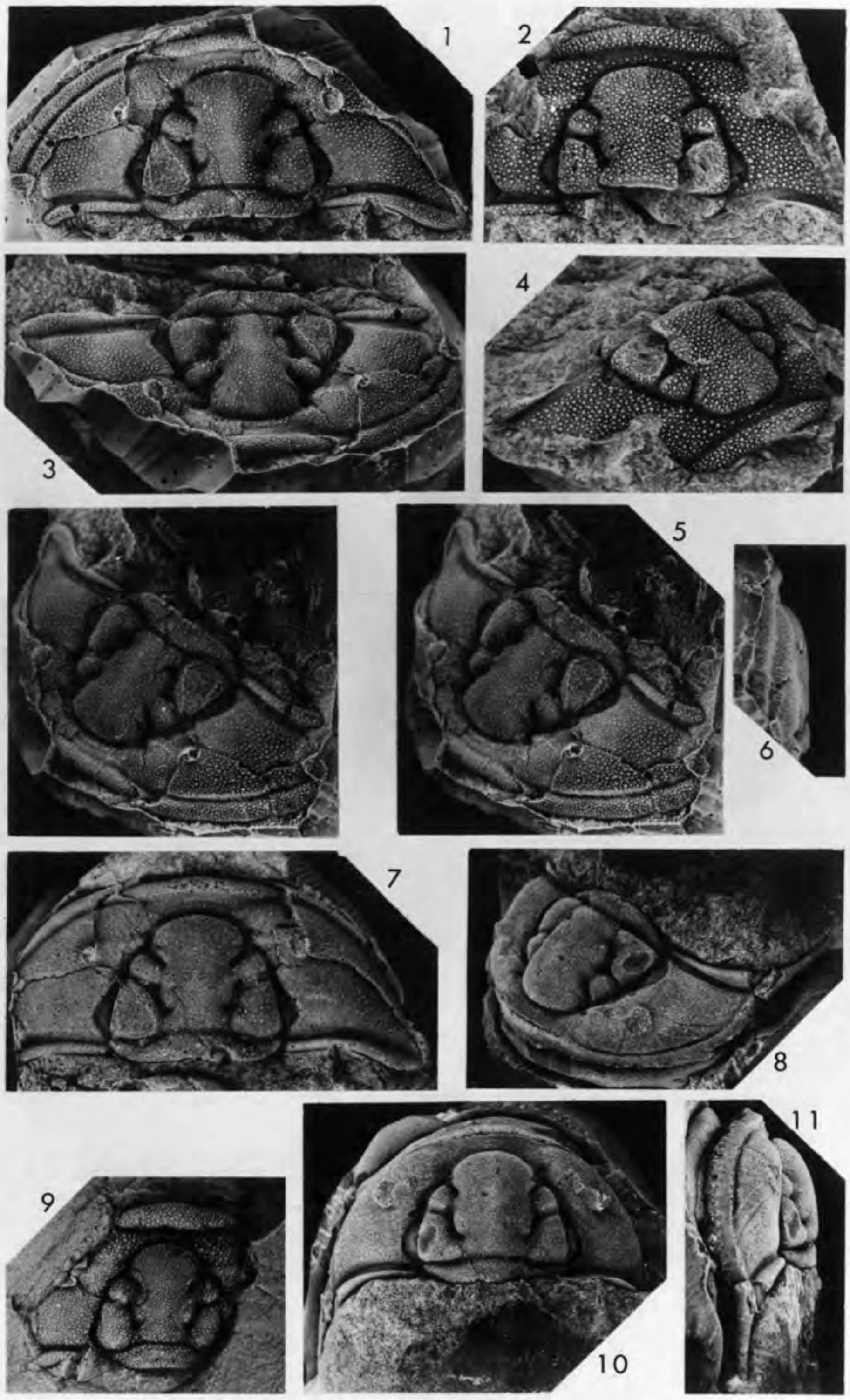

PLATE 2

Figs. 1-6. Pharostoma pulchrum pulchrum (Beyrich, 1846)

1, 2, 6. Lectotype, incomplete cranidium, 'Silcoset' rubber cast of external mould, MB 303 B.K., Letna Formation (lower Caradoc), Vesela, Czechoslovakia. Dorsal, frontal stereo-pairs, right oblique view, x 2. Figured Beyrich 1846, pl. 2, figs. 6a, b as Calymene pulchra.

3-5. Paralectotype, incomplete cephalon, MB 501 B.K, Letna Formation (lower Caradoc), Vesela, Czechoslovakia. Dorsal, frontal stereo-pairs, left oblique view, x $1\frac{1}{2}$. Figured Beyrich 1846, pl. 2, figs. 6a, b.

2

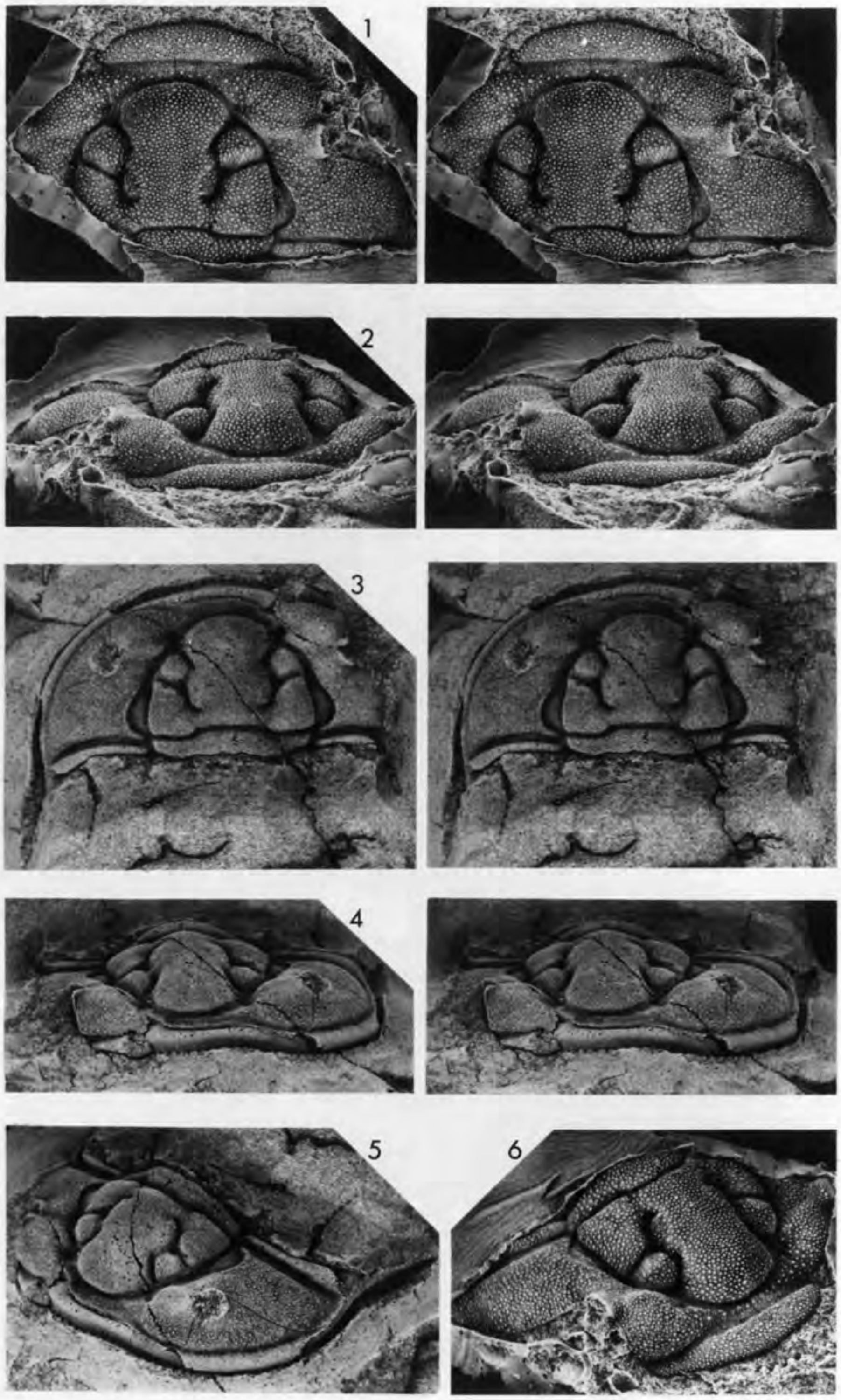

PLATE 3

Figs. 1-8. Pharostoma pulchrum pulchrum (Beyrich, 1846)

1-4. Almost complete cranidium, internal mould, BM I5422, Letna Formation (lower Caradoc), Vesela, Czechoslovakia. Dorsal, frontal stereo-pairs, right oblique, right lateral views, x 2.

5, 7, 8. Paralectotype, pygidium, internal mould, MB 264 B.K./k191, Letna Formation (lower Caradoc), Vesela, Czechoslovakia. Dorsal view, posterior stereo-pair, right lateral view, x 2. Figured Beyrich 1846, pl. 2, fig. 6d as Calymene pulchra.

6. Complete specimen minus free cheeks, internal mould, BM I665, ? Letna Formation, Trubska, Czechoslovakia. Dorsal view, x $1\frac{1}{4}$.

3

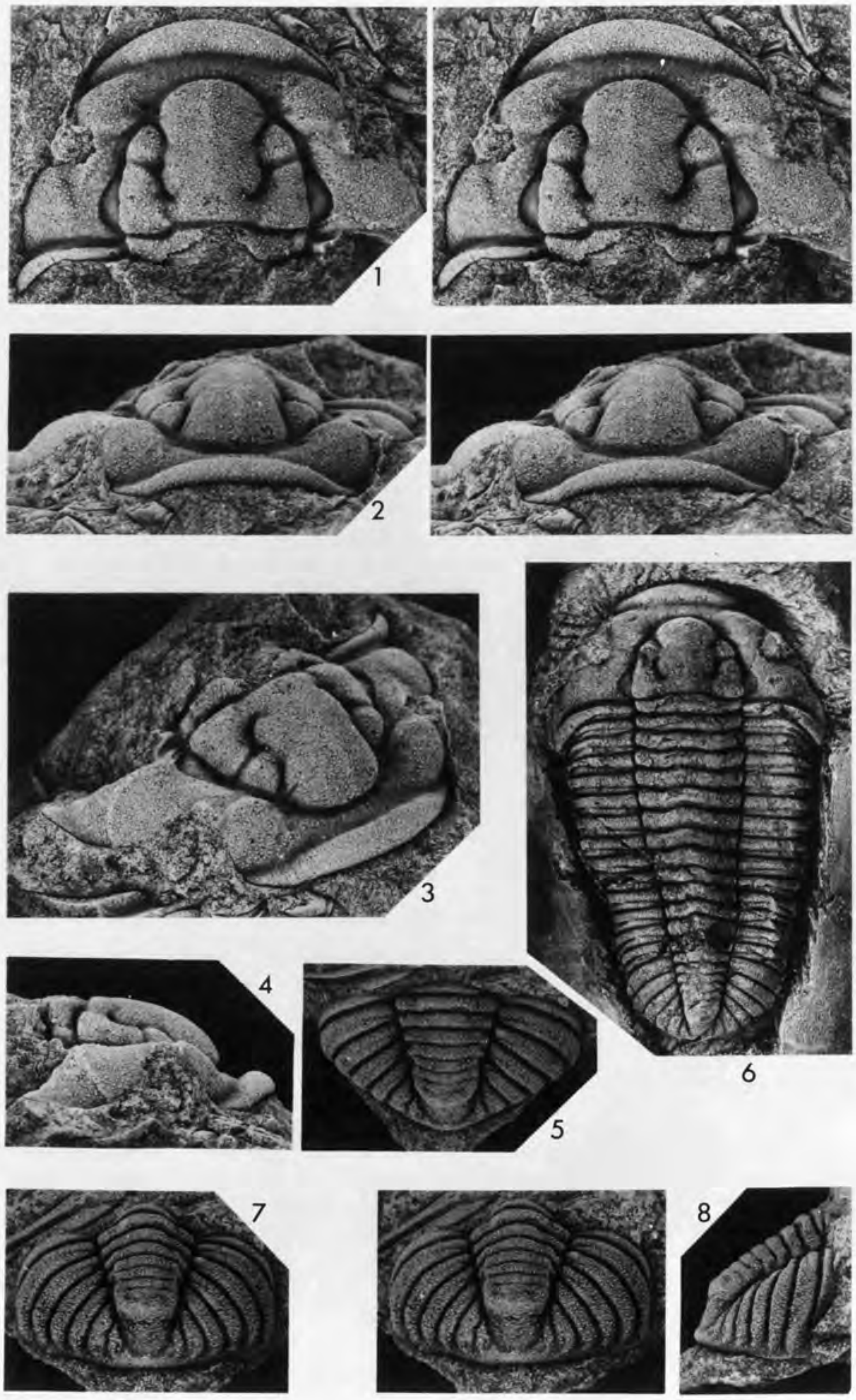

PLATE 4 (continued)

Fig. 5. Pharostoma cf. P. nieszkowskii (Schmidt, 1894)

Cranidium and several attached thoracic segments, internal mould, PMO 91024, Lower Chasmops Shale, trackside cutting, NE side of Semsvannet, Asker district. Coll. J.F. Bockelie, 1965. Dorsal view, x 4.

PLATE 4

Figs. 1, 2, 6, 9. Pharostoma pulchrum subsp. nov. A

1. Poorly preserved, almost complete specimen, plaster cast of internal mould, NMP It324 CD1167, Zahorany Formation (middle Caradoc), Zahorany, Czechoslovakia. Dorsal view, x 1¾. Figured Barrande 1852, pl. 19, fig. 2 (plate reversed). 'Lectotype' selected by Snajdr (1956) of 'P. pulchrum pulchrum (Barrande, 1846)'.

2, 9. Incomplete cranidium, DJS/139, Zahorany Formation, Lodenice, Czechoslovakia. Coll. L. Marek. Left lateral view, dorsal stereo-pair, x 1¾.

6. Poorly preserved specimen, plaster cast of internal mould, NMP It325 CD1166, Zahorany Formation (middle Caradoc), Zahorany, Czechoslovakia. Dorsal view, x 1¾. Figured Barrande 1852, pl. 19, fig. 3 as 'Calymene pulchra Barr'.

Figs. 3, 4, 7, 8. Pharostoma pulchrum pulchrum (Beyrich, 1846)

3, 7. Paralectotype, free cheek, internal mould (fig. 3) and 'Silcoset' rubber cast of internal mould (fig. 7), MB 502 B.K./190, Letna Formation (lower Caradoc), Vesela, Czechoslovakia. Dorsal and ventral views, x 2. Figured Beyrich 1846, pl. 2, fig. 6c as Calymene pulchra.

4, 8. Pygidium, 'Silcoset' rubber cast of external mould, NMP It331, Letna Formation, Vesela, Czechoslovakia. Dorsal view, posterior stereo-pair, x 2½. Additional specimen used by Barrande 1852, pl. 19, fig. 9.

4

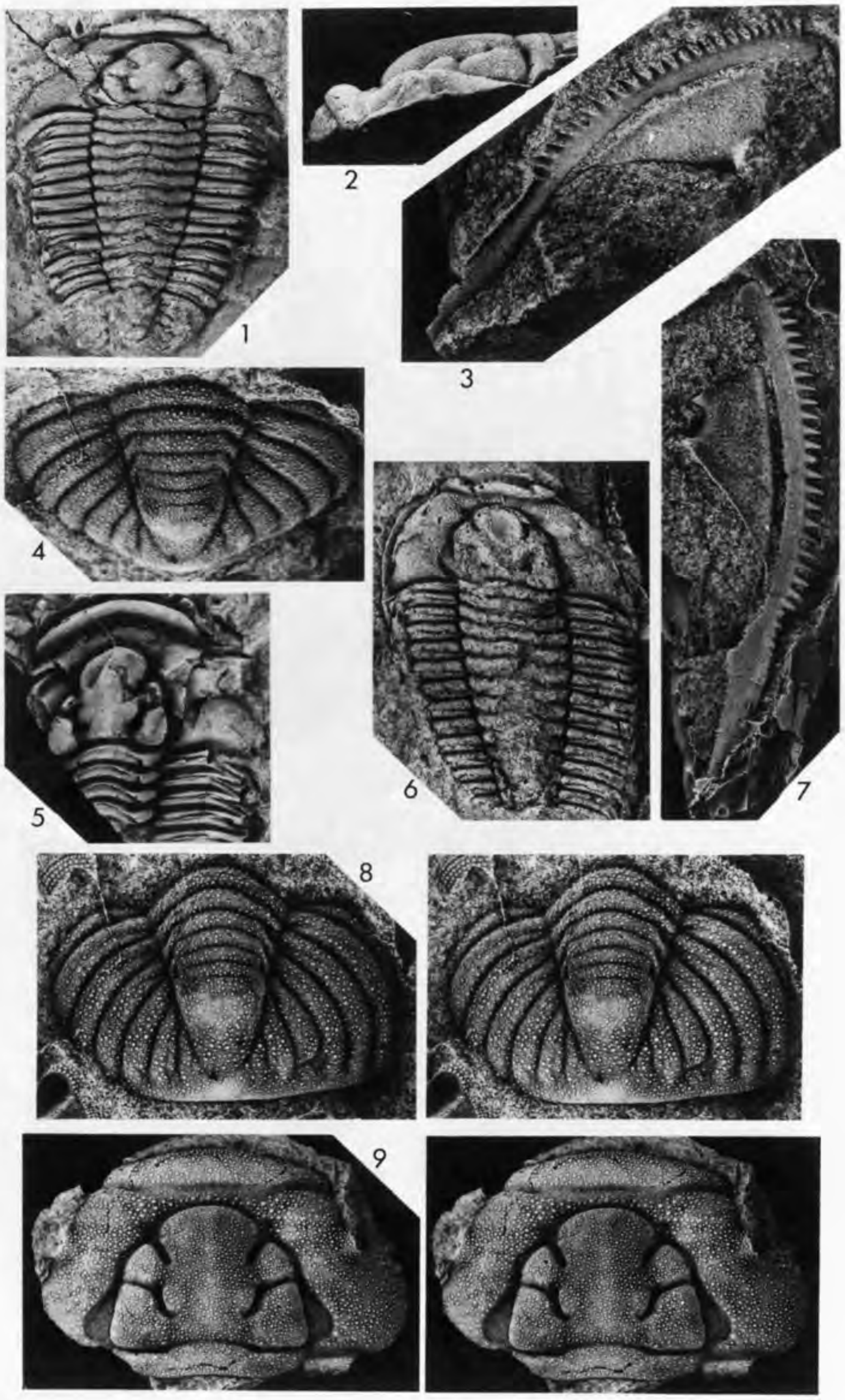

PLATE 5

Figs. 1-4. Pharostoma aff. P. denticulatum (Eichwald, 1860)

Incomplete cranidium, RM Ar10692, Raniceps Limestone, Utby, Dalarna, Sweden. Coll. G. Holm, 1880. Dorsal stereo-pair, right lateral view, right oblique stereo-pair, anterodorsal view, x 6.

Figs. 5-7, 9. Pharostoma nieszkowskii (Schmidt, 1894)

5, 6, 9. Incomplete cranidium, partially exfoliated, RM Ar34406, Kukruse Stage (= zone of Nemagraptus gracilis), Kukruse, Estonia. Coll. G. Holm, 1883. Right lateral, right oblique views, dorsal stereo-pair, x 6.

7. Incomplete cranidium, partially exfoliated, RM Ar34361, Kukruse Stage, Vanamoisa, Estonia. Dorsal view, x 12.

Fig. 8. Pharostoma cf. P. nieszkowskii (Schmidt, 1894)

Incomplete cranidium, internal mould, PMO 91025, Lower Chasmops Shale, trackside cutting, NE side of Semsvannet, Asker district. Coll. D.J. Siveter, 1971. Dorsal view, x 6.

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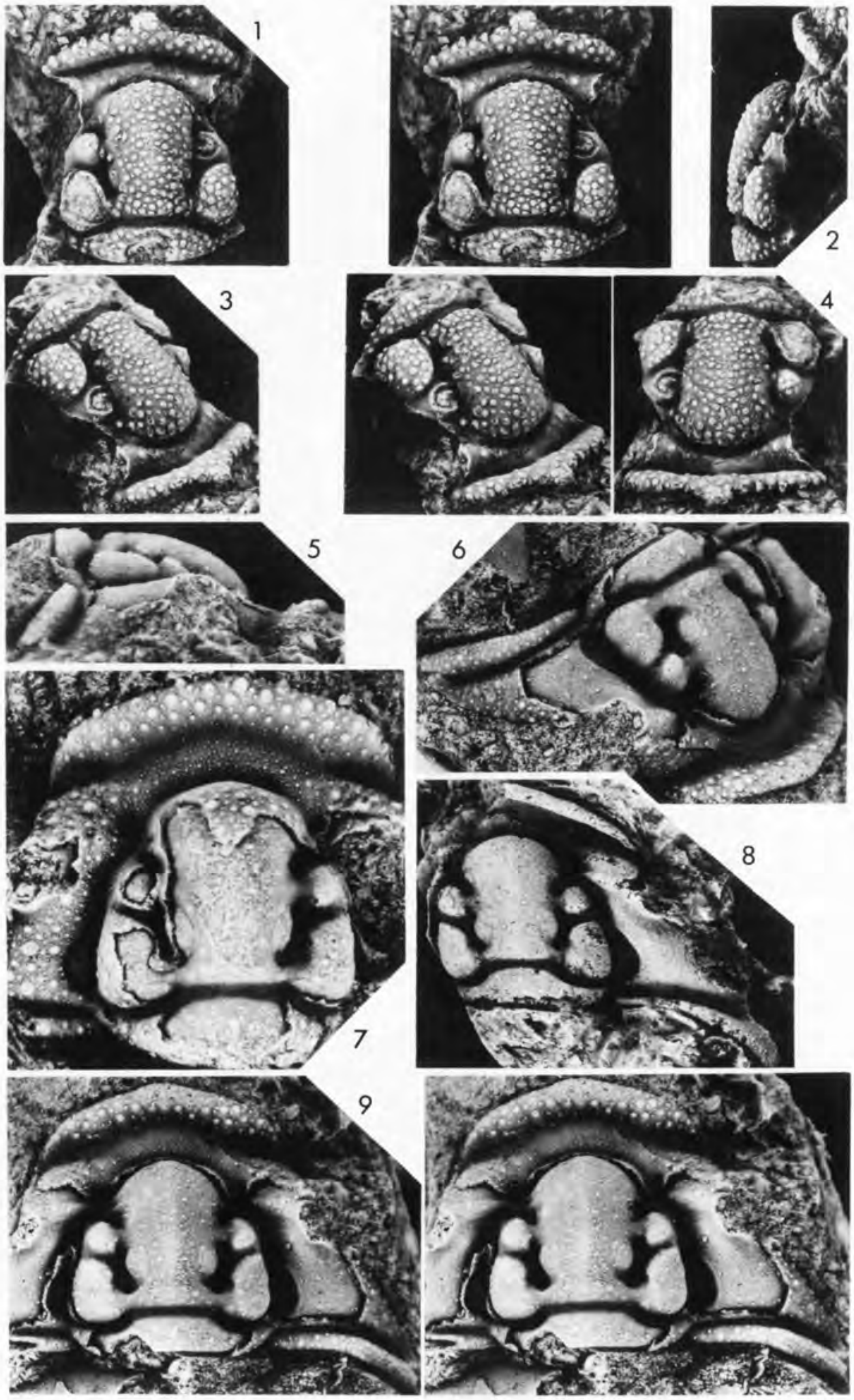

PLATE 6

Figs. 1-3, 5, 6. Pharostoma nieszkowskii (Schmidt, 1894)

1, 2, Incomplete cranidium, internal mould, IPLU L02955t,
5. 'Ampyx' Limestone middle Ordovician, Tommarp, SE Scania. Dorsal, left lateral, frontal views, x 6. Figured Funkquist 1919, pl. 1, fig. 5 as Calymmene pulchra Beyrich.

3, 6. Incomplete pygidium, internal mould, IPLU L02956t, 'Ampyx' Limestone, middle Ordovician, Tommarp, SE Scania. Right oblique view, x 8; posterior view, x 6.

Figs. 4, 7-12. Pharostoma simile Thorslund, 1940

4, 9. Holotype, cranidium, IPU Ar2469, Lower Chasmops Limestone, Island of Ringsön, SE of Tvaren, Södermanland, Sweden. Dorsal stereo-pair, left oblique view, x 2½. Figured Thorslund, 1940, pl. 11, fig. 1.

7, 11. Thoracic segment, IPU Ar2479, same horizon and locality as for fig. 4. Dorsal, right lateral views, x 2½. Figured Thorslund, 1940, pl. 11, figs. 13, 14.

8. Pygidium, IPU Ar2476, same horizon and locality as for fig. 4. Dorsal view, x 12. See also Pl. 7, fig. 3. figured Thorslund 1940, pl. 11, fig. 9.

10, 12. Incomplete hypostome, partially exfoliated, IPU Ar2475, same horizon and locality as for fig. 4. Ventral stereo-pair, lateral view, x 4½. Figured Thorslund 1940, pl. 11, fig. 8.

6

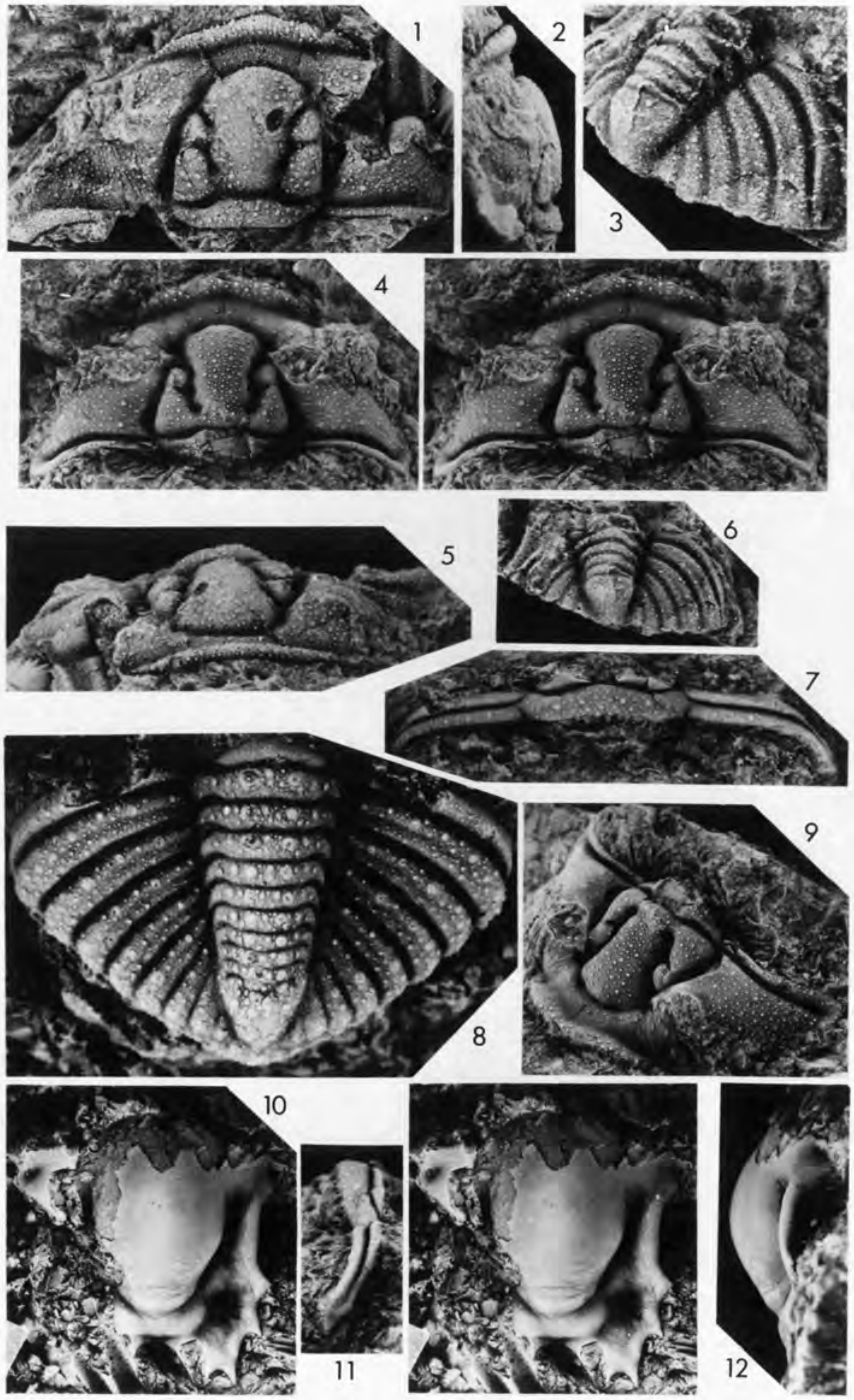

PLATE 7

Figs. 1-10. Pharostoma simile Thorslund, 1940

1. Incomplete hypostome, partially exfoliated, IPU Ar2474, Lower Chasmops Limestone, Island of Ringsön, SE of Tvaren, Södermanland, Sweden. Ventral stereo-pair, x 4½. Figured Thorslund, 1940, pl. 11, fig. 7.

2. Incomplete hypostome, partially exfoliated, IPU Ar2473, same horizon and locality as for fig. 1. Ventral view, x 4½.

3. Pygidium, IPU Ar2476, same horizon and locality as for fig. 7. Left oblique view, x 12. See also Pl. 6, fig. 8. Figured Thorslund,1940, pl. 11, fig. 9.

4. Incomplete cranidium, IPU Ar2467, same horizon and locality as for fig. 1. Dorsal view, x 4½. Figured Thorslund,1940, pl. 11, fig. 12.

5, 7, 8. Incomplete cranidium, IPU Ar2468, same horizon and locality as for fig. 1. Anterodorsal view, dorsal stereo-pair, right lateral view, x 1.8. Figured Thorslund,1940, pl. 11, figs. 2, 3.

6. Incomplete cranidium, RM Ar9150, loose block of Ordovician age, Ytterhallen, Jamtland. Dorsal view, x 2.

10. Free cheek, doublure and lateral marginal spines are in internal mould form, IPU Ar2470, same horizon and locality as for fig. 1. Dorsal stereo-pair, x 4½. Figured Thorslund, 1940, pl. 11, fig. 4.

9. Doublure and lateral marginal spines of free cheek, IPU Ar2472, same horizon and locality as for fig. 1. Ventral view, x 4½. Figured Thorslund, 1940, pl. 11, fig. 5.

7

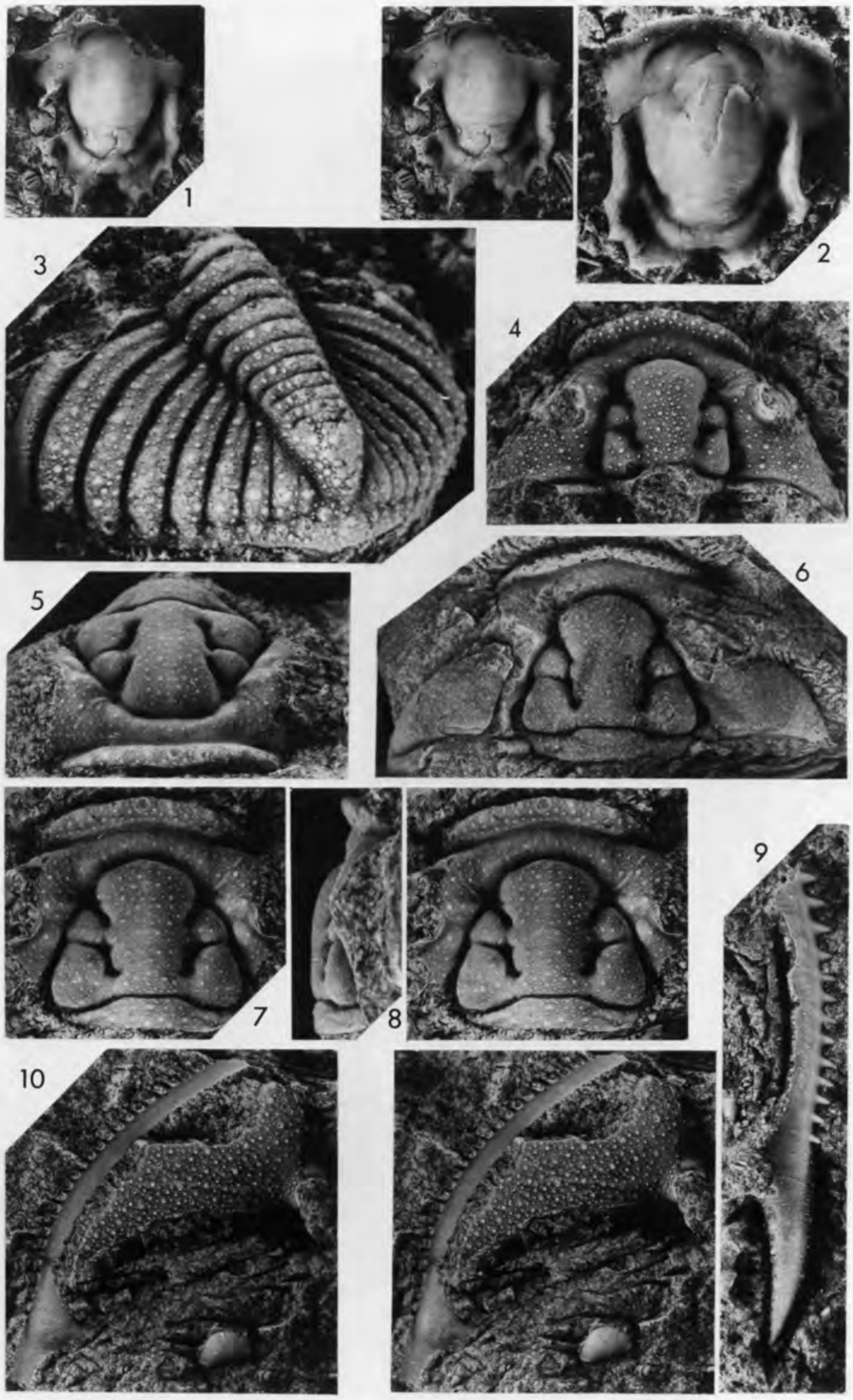

PLATE 8

Figs. 1, 2, 4. Pharostoma simile Thorslund, 1940

Pygidium, IPU Ar2478, Lower Chasmops Limestone, Island of Ringsön, SE of Tvaren, Södermanland, Sweden. Dorsal view, right lateral view, posterior stereo-pair, x 4½. Figured Thorslund, 1940, pl. 11, fig. 11.

Fig. 3. Pharostoma sp. indet 2

Incomplete cranidium with the remains of nine thoracic segments, RM Ar23608, Dalby Limestone (zone of Nemagraptus gracilis), Böda Hamn, Öland. Dorsal view, x 2.

Figs. 5-11. Pharostoma foveolatum (Törnquist, 1884)

5-8 Holotype, incomplete cranidium, SGU unnumbered, Kullsberg Limestone, Furudal, Dalarna, Sweden. Dorsal stereo-pair, right lateral, right oblique, anterodorsal views, x 2½. Coll. G. Schmalensee. Figured Törnquist, 1884, pl. 1, fig. 45, and Warburg, 1925, pl. 4, fig. 16.

9-11. Pygidium, IPU Ar465, Kullsberg Limestone, Skalberget, N of Glisstjarn, Dalarna, Sweden. Dorsal view, posterior stereo-pair, right lateral view, x 1.

8

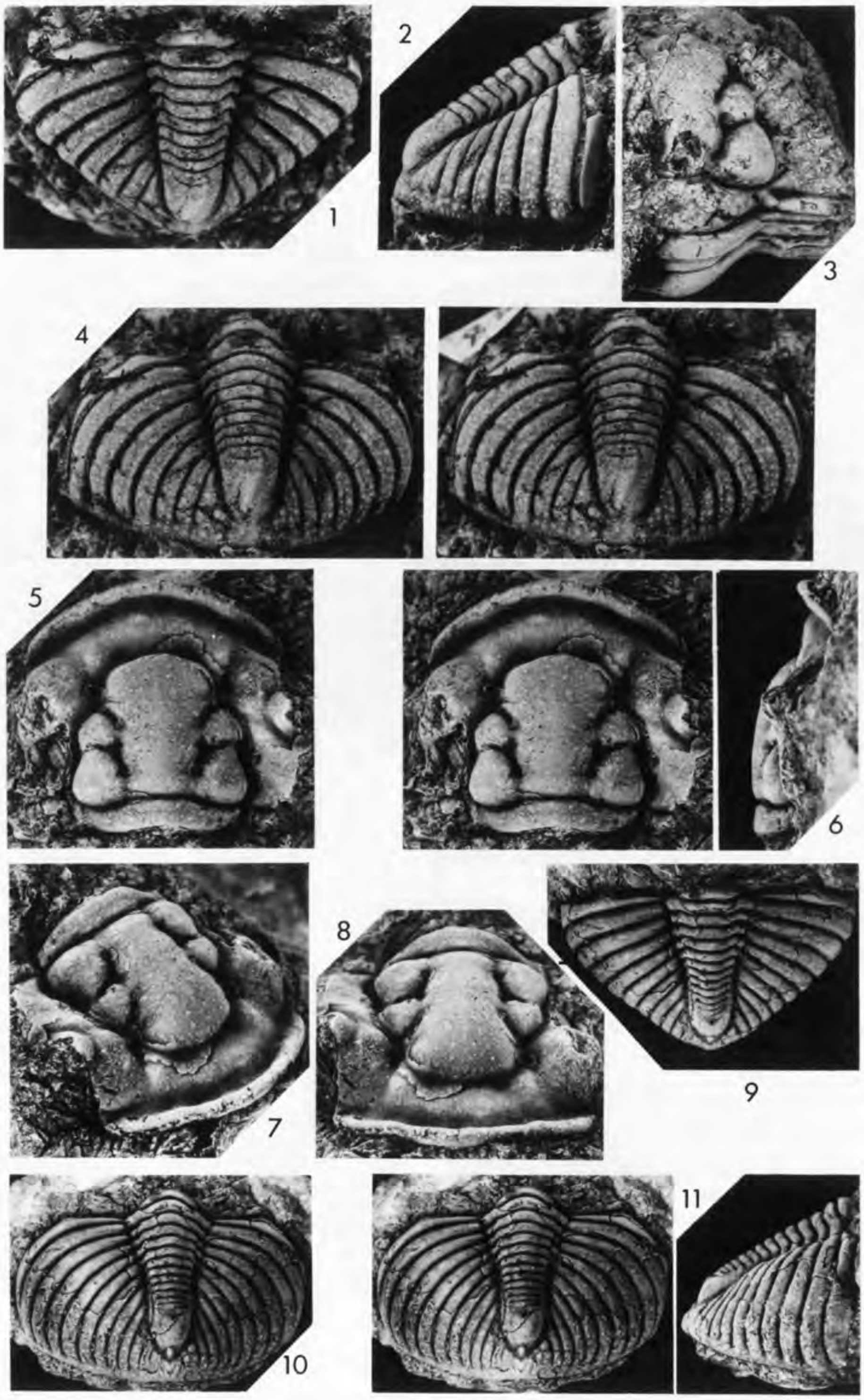

PLATE 9

Figs. 1-3, 5-7. <u>Pharostoma</u> <u>foveolatum</u> (Törnquist, 1884)

1-3, 5. Large incomplete cephalon, IPU Ar469, Kullsberg Limestone, Kullsberg, Dalarna, Sweden. Dorsal, anterodorsal stereo-pairs, left oblique, right lateral views, x 1.

6, 7. Incomplete pygidium, IPU Ar465, Kullsberg Limestone, Kullsberg, Dalarna, Sweden. Coll. E. Warburg, 1916. Dorsal stereo-pair, left lateral view, x 1. See also Pl. 10, fig. 2.

Fig 4. <u>Pharostoma</u> cf. <u>P.</u> <u>foveolatum</u> (Törnquist, 1884)

Incomplete cranidium, PMO 38556, beds above the coral limestone, Mjøsa Limestone, peninsular S of Bergvika, Helgøya, Nes-Hamer district, Oslo Region, Norway. Coll. J. Kiaer, 1922. Dorsal view, x 12.

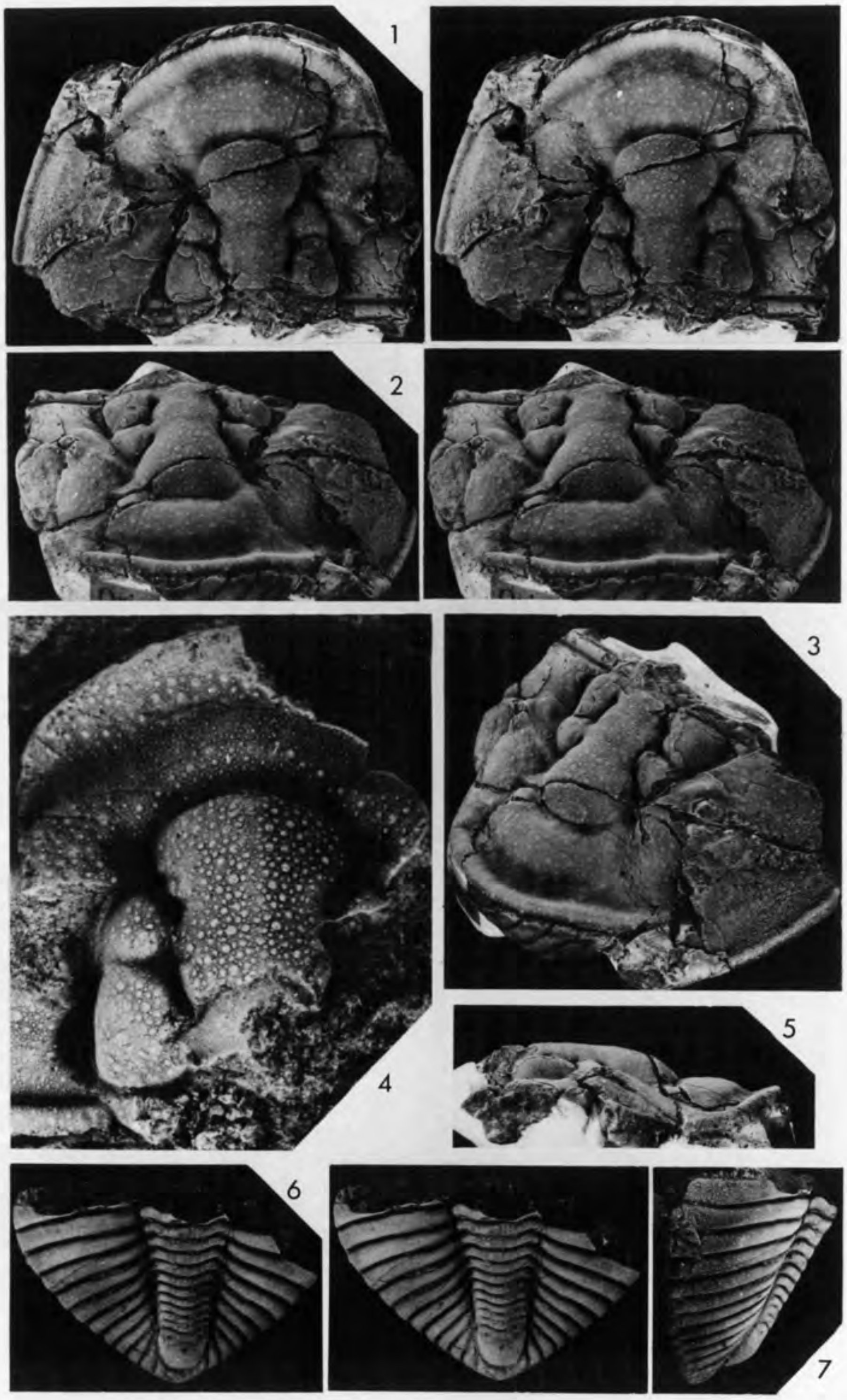
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PLATE 10

Figs. 1, 6. Pharostoma narinosum sp. nov.

1. Holotype, incomplete cranidium, PMO 81266, Upper Chasmops Limestone, S side of N Raudholmen (= Raudskjaer), Oslo-Asker district, Oslo Region, Norway. Coll. N. Spjeldnaes, 1953. Dorsal view, x 6.

6. Incomplete cranidium, PMO 91448, Upper Chasmops Limestone, one metre below the Lower Tretaspis Shale, SE end of Kalvøya, Baerum, Oslo-Asker district. Coll. D.J. Siveter & D.L. Bruton, 1971. Left lateral view, x 3.

Fig. 2. Pharostoma foveolatum (Törnquist, 1884)

Incomplete pygidium, IPU Ar465, Kullsberg Limestone, Kullsberg, Dalarna, Sweden. Coll. E. Warburg, 1916. Left oblique view, x 1.

Figs. 3, 4, 5, 7. Pharostoma oelandicum Angelin, 1854

Holotype, incomplete cranidium, partially exfoliated, RM Ar2285, glacial erratics of the Macrourus Limestone (middle Ordovician), Öland. Anterodorsal view, dorsal, right oblique stereo-pair, right lateral view, x 4. Figured Angelin, 1854, pl. 33, figs. 15, 15a.

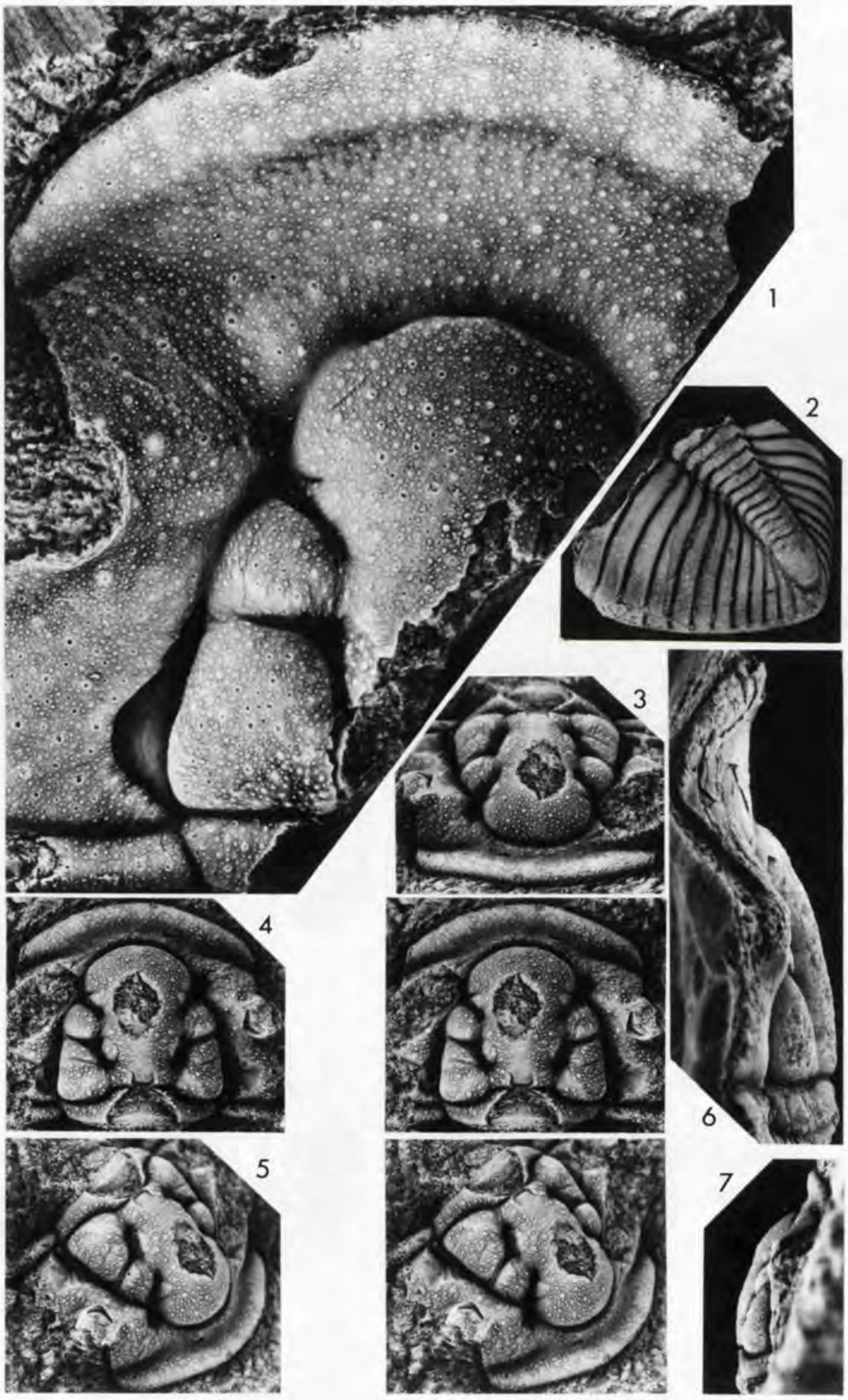
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PLATE 11 (continued)

Fig. 9. Pharostoma sp. B

Incomplete, distorted cranidium, 'Silcoset' rubber cast of external mould, PMO 81538, Upper Chasmops Shale, Hvalstad skjaeringen, Oslo-Asker district, Oslo Region, Norway. Coll. N. Spjeldnaes, 1957. Dorsal view, x 8.

Fig. 10. Pharostoma sp. A

Cranidium, PMO 81312, 1.7 metres below the top of the Upper Chasmops Limestone, N Raudsjaer, Oslo-Asker district, Oslo Region, Norway. Coll. Nikolaisen, Bruton, Hamar, 1967. Dorsal view, x 6.

PLATE 11

Figs. 1-7. <u>Pharostoma</u> <u>ornithoreos</u> sp. nov.

1, 2, 6, 7. Holotype, incomplete cranidium, partially exfoliated, BM It8931, Birdshill Limestone, Pusgillian Stage, Ashgill Series, quarry 200 yards NW of Birdshill Farm, $1\frac{1}{2}$ miles WNW of Llandeilo, Carmarthenshire, S Wales. Coll. S.F. Morris, 1965. Dorsal, frontal stereo-pairs, right oblique, right lateral views, x 4.

3. Incomplete cranidium, 'Silcoset' rubber cast of external mould, BM It8933, same horizon, locality and collector as for fig. 1. Dorsal view, x 4.

4 Incomplete cranidium, partially exfoliated, BM It8930, same horizon, locality and collector as for fig. 1. Dorsal view, x 4.

5. Incomplete cranidium, partially exfoliated, BM It8934, same horizon, locality and collector as for fig. 1. Dorsal view, x 6.

Fig. 8. <u>Pharostoma</u> cf. <u>P.</u> <u>ornithoreos</u> sp. nov.

Incomplete cranidium, cuticle lacking except on preglabellar field, BM unnumbered, Sholeshook Limestone, Cautleyan Stage, Ashgill Series, quarry at Sholeshook Farm, one mile ENE of Haverfordwest, Pembs. Coll. S.F. Morris, 1965. Dorsal view, x 6.

11

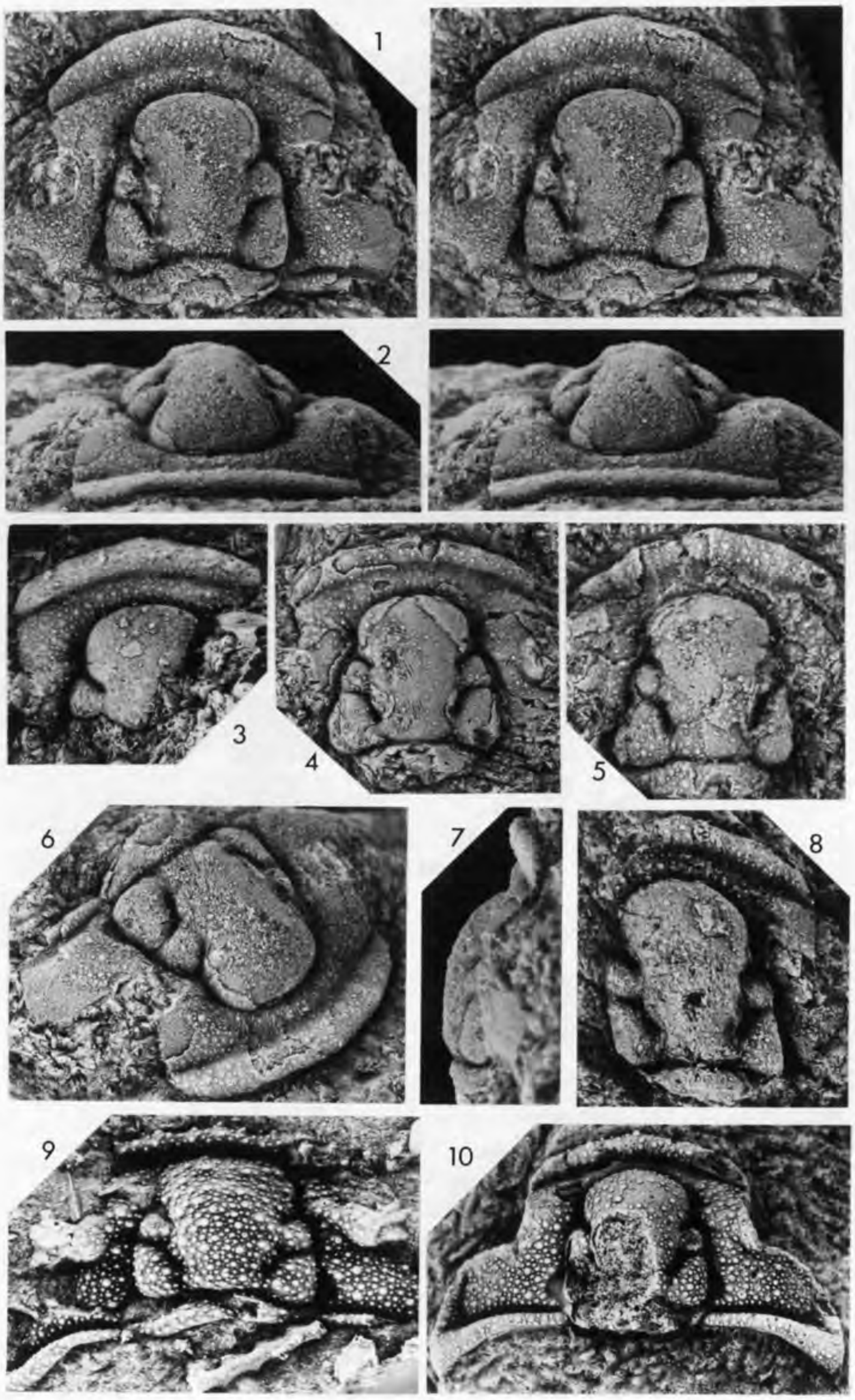

PLATE 12

Figs. 1, 2, 4-6, 11, 13. Pharostoma obtusum (McCoy, 1846)

1, 2, 4. Incomplete cranidium, RM Ar47709, Boda Limestone, Kallholn, Dalarna, Sweden. Dorsal stereo-pair, left lateral view, anterodorsal view, x 6.

5, 11. Incomplete cranidium, RM Ar43629, same horizon and locality as for fig. 1. Dorsal, right lateral views, x 6.

6. Incomplete cranidium, RM Ar43612, same horizon and locality as for fig. 1. Coll. Isberg. Dorsal view, x 6.

13. Incomplete cranidium, BM It1832, Kildare Limestone, late Ashgill Series, A.D. Wright MS loc. 3b, near the Chair of Kildare, SW of Dublin, Eire. Coll. W.T. & J.F. Dean, 1964. Dorsal stereo-pair, x 6. Figured Dean 1971, pl. 18, figs. 6, 8, 15 as Prionocheilus obtusus (McCoy).

Figs. 3, 9, 14. Pharostoma leptaenarum ? (Törnquist, 1884)

Cranidium, 'Silcoset' rubber cast of external mould (figs. 3, 14) and internal mould (fig. 9), IPLU LO1938t, Trinucleus Beds of Olin (1906), middle Ashgill Series, Tosterup, Scania. Dorsal, right lateral views, x 3½. Internal mould was figured Olin 1906, pl. 2, fig. 15 as Calymene pulchra Beyrich.

Figs. 7, 8, 10, 12. Pharostoma leptaenarum (Törnquist, 1884)

7, 8, 12. Holotype, incomplete cranidium, IPLU LO593t, Boda Limestone, Boda, Dalarna, Sweden. Left lateral, dorsal, left oblique views, x 7. Figured Törnquist, 1884, pl. 1, fig. 44 as Calymene leptaenarum n. sp.

10. Incomplete cranidium, IPLU unnumbered, same horizon and locality as for fig. 7. Part of Törnquists material. Dorsal view, x 7.

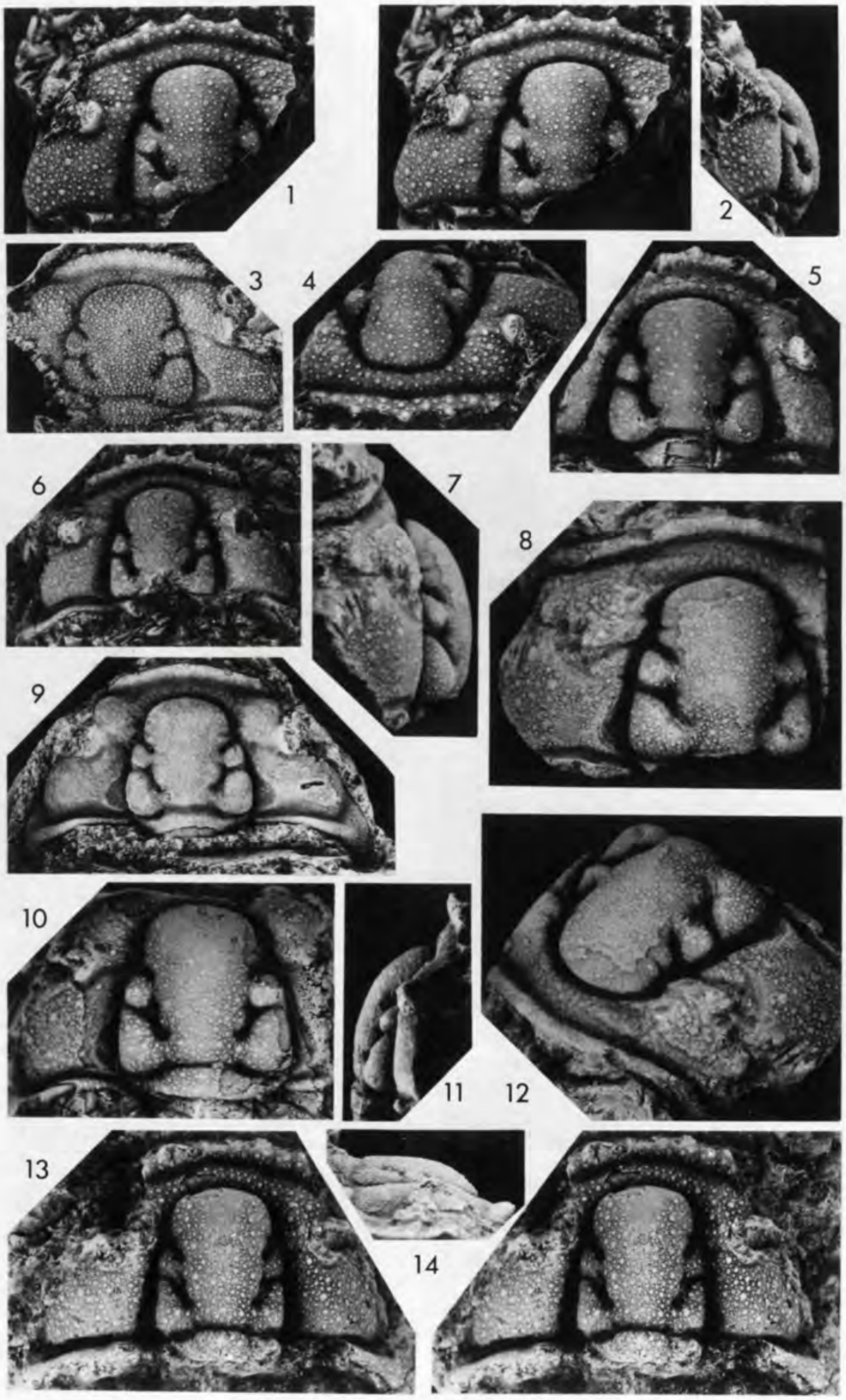
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PLATE 13

Figs. 1-8. Thulincola barbarus Tripp, 1962

1, 5, Incomplete cranidium, BM In23399 (Gray Colln.),
7, 8. Balclatchie Conglomerate (lower Caradoc), Balclatchie Girvan district. Right oblique, right lateral, frontal views, dorsal stereo-pair, x 10. Referred to by Reed (1906, p. 138) as Calymene sp. ind. (b).

2, 6. Holotype, incomplete cranidium, internal mould, HM A5345a, decalcified light-brown weathered mudstone, E end of small wood on brow of Kirkdominae Hill, Girvan district (Nat. Grid. Ref. NX 225000/592100). Figured Tripp 1962, pl. 4, figs. 1 a, b.

3. Incomplete cranidium, BM In23398 (Gray Colln.), same horizon and locality as for fig. 1. Dorsal view, x 10. Referred to by Reed (1906, p. 138) as Calymene sp. ind. (a).

4. Incomplete cranidium, HM A5346a, same horizon and locality as for fig. 2. Figured Tripp 1962, pl. 4, fig. 4.

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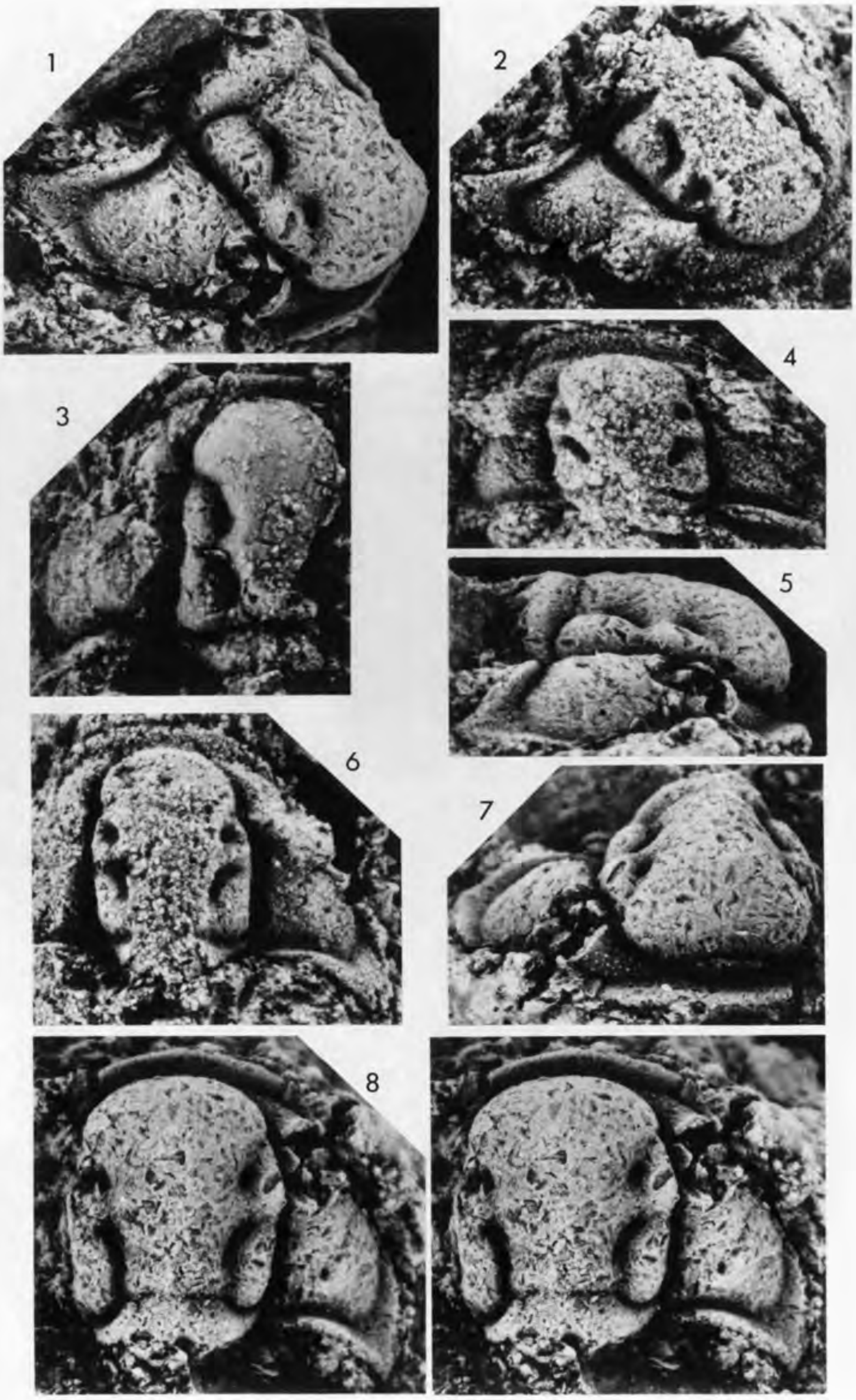

CHAPTER B PLATES 1-11

CALYMENID TRILOBITES FROM THE MIDDLE ORDOVICIAN OF THE OSLO REGION, NORWAY.

PLATE 1 (continued)

Figs. 6, 7. Pharostoma cf. P. foveolatum (Törnquist, 1884)

6. Incomplete cranidium, PMO 38556, beds above the coral limestone, Mjøsa Limestone (4bδ +), peninsular S of Bergvika, Helgøya, Nes-Hamar district. Coll. J. Kiaer, 21. 9. 1922. Dorsal stereo-pair, x 6.

7. Incomplete cranidium, PMO 38555, same horizon, locality and collector as for fig. 6. Dorsal view, x 8.

PLATE 1

Figs. 1-5, 8, 9. Pharostoma cf. P. nieszkowskii (Schmidt, 1894)

1, 2. Internal mould cranidium, PMO 91025, Lower Chasmops Shale (4bα), trackside cutting, NE side of Semsvannet, Asker district. Coll. D.J. Siveter, 7. 10. 1971. Dorsal stereo-pair, right oblique view, x 6.

3. Internal mould cranidium with several thoracic segments, PMO 91024 (on same block as fig. 5), Lower Chasmops Shale (4bα), same horizon and locality as fig. 1. Coll. J.F. Bockelie, 28. 8. 1965. Dorsal view, x 4.

4. Internal mould cranidium, PMO 91020, Lower Chasmops Shale (4bα), same horizon and locality as fig. 1. Coll. J.F. Bockelie, 18. 10. 1967. Dorsal view, x 8.

5. Internal mould cranidium, PMO 91024 (on same block as fig. 3), same horizon, locality and collector as for fig. 3. Dorsal view, x 8.

8. 'Silcoset' rubber cast of external mould pygidium, PMO 91030, Lower Chasmops Shale (4bα), same horizon and locality as fig. 1. Coll. J.F. Bockelie, D.L. Bruton, D.J. Siveter, 7. 10. 1971. Posterior stereo-pair, x 8.

9. Internal mould pygidium, PMO 91027, same horizon, locality and collectors as for fig. 8. Posterior view, x 6.

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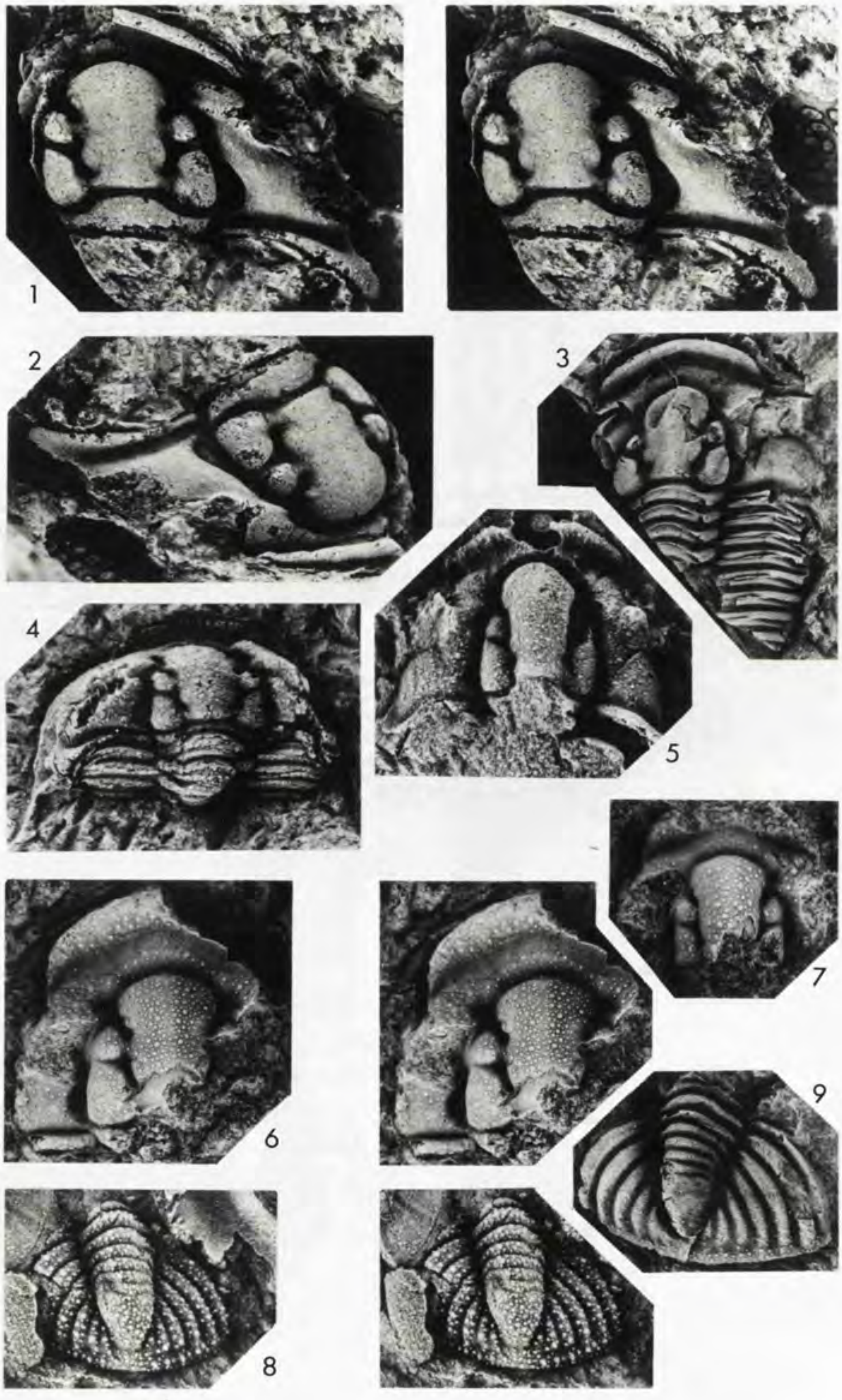

PLATE 2

Figs. 1-8. *Pharostoma narinosum* sp. nov.

1-4. Holotype, incomplete cranidium, PMO 81266, Upper *Chasmops* Limestone (4bδ), S side of N Raudholmen (=Raudskjaer), Oslo-Asker district. Coll. N. Spjeldnaes, 1953. Dorsal stereo-pair, frontal stereo-pair, left oblique, left lateral views, x 2.

5, 7. Incomplete cranidium, much of cuticle missing except for preglabellar field, PMO 91448, Upper *Chasmops* Limestone (4bδ), one metre below the Lower *Tretaspis* Shale (4cα), SE end of Kalvøya, Baerum, Oslo-Asker district. Coll. D.J. Siveter & D.L. Bruton 1971. Left lateral, dorsal views x 2.

6, 8. Incomplete cranidium, PMO 91449, same horizon, locality and collectors as for fig. 5. Left oblique, dorsal views, x 2.

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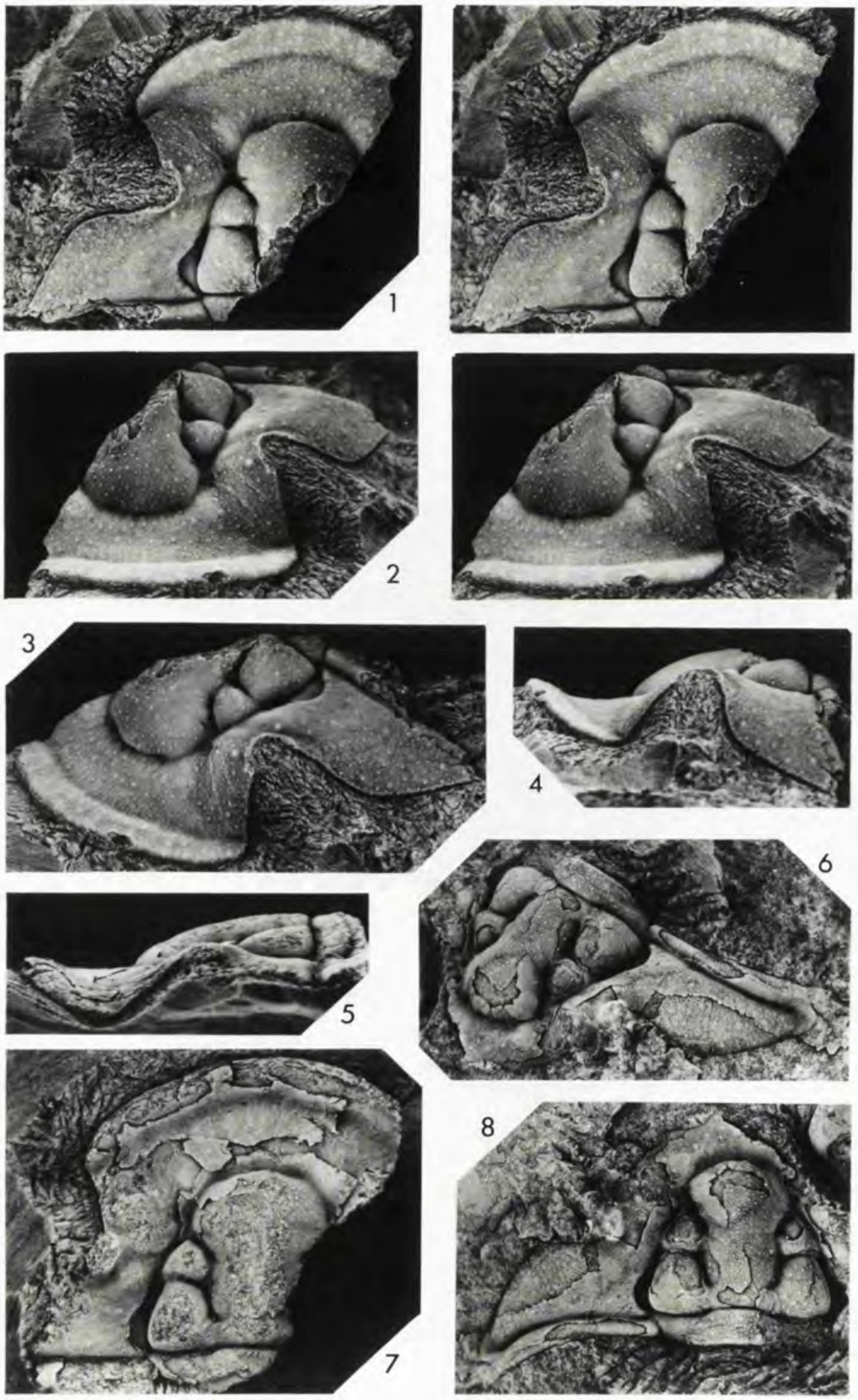

PLATE 3.

Figs. 1, 4-7 *Pharostoma* sp. A.

1, 4. Cranidium, PMO 81312 (on same block as figs. 5-7), 1.7 metres below the top of the Upper *Chasmops* Limestone (4bδ), N Raudsjaer, Oslo-Asker district. Coll. Nikolaisen, Bruton, Hamar, 1967. Dorsal stereo-pair, right oblique view, x 6.

5-7. Incomplete cranidium, PMO 81312 (on same block as figs. 1, 4), same horizon, locality and collectors as for figs. 1, 4. Dorsal and left oblique views, x 6; left lateral view, x 9.

Figs. 2, 3. *Pharostoma* sp. B.

2. 'Silcoset' rubber cast of external mould cranidium, PMO 81538, Upper *Chasmops* Shale (4bγ), Hvalstad Skjaeringen, Oslo-Asker district. Coll. N. Spjeldnaes, 28. 4. 1957. Dorsal view, x 8.

3. 'Silcoset' rubber cast of external mould cranidium, PMO 81535, same horizon, locality and collector as for fig. 2. Dorsal view, x 6.

Figs. 8-11. *Flexicalymene jemtlandica* Thorslund, 1940

8. Incomplete cranidium, PMO 81112/9/2, 1.8 metres under the top of the Upper *Chasmops* Limestone (4bδ), N. Raudskjaer, Oslo-Asker district. Coll. F. Nikolaisen, 19. 9. 1968. Frontal view, x 4. See also Pl. 4, figs. 4, 8, 9.

9-11. Incomplete cranidium, PMO 81308, 1.7 metres under the top of the Upper *Chasmops* Limestone (4bδ), N. Raudskjaer, Oslo-Asker district. Coll. Nikolaisen, Bruton, Hamar, 1967. Left oblique, dorsal, left lateral views, x 3.

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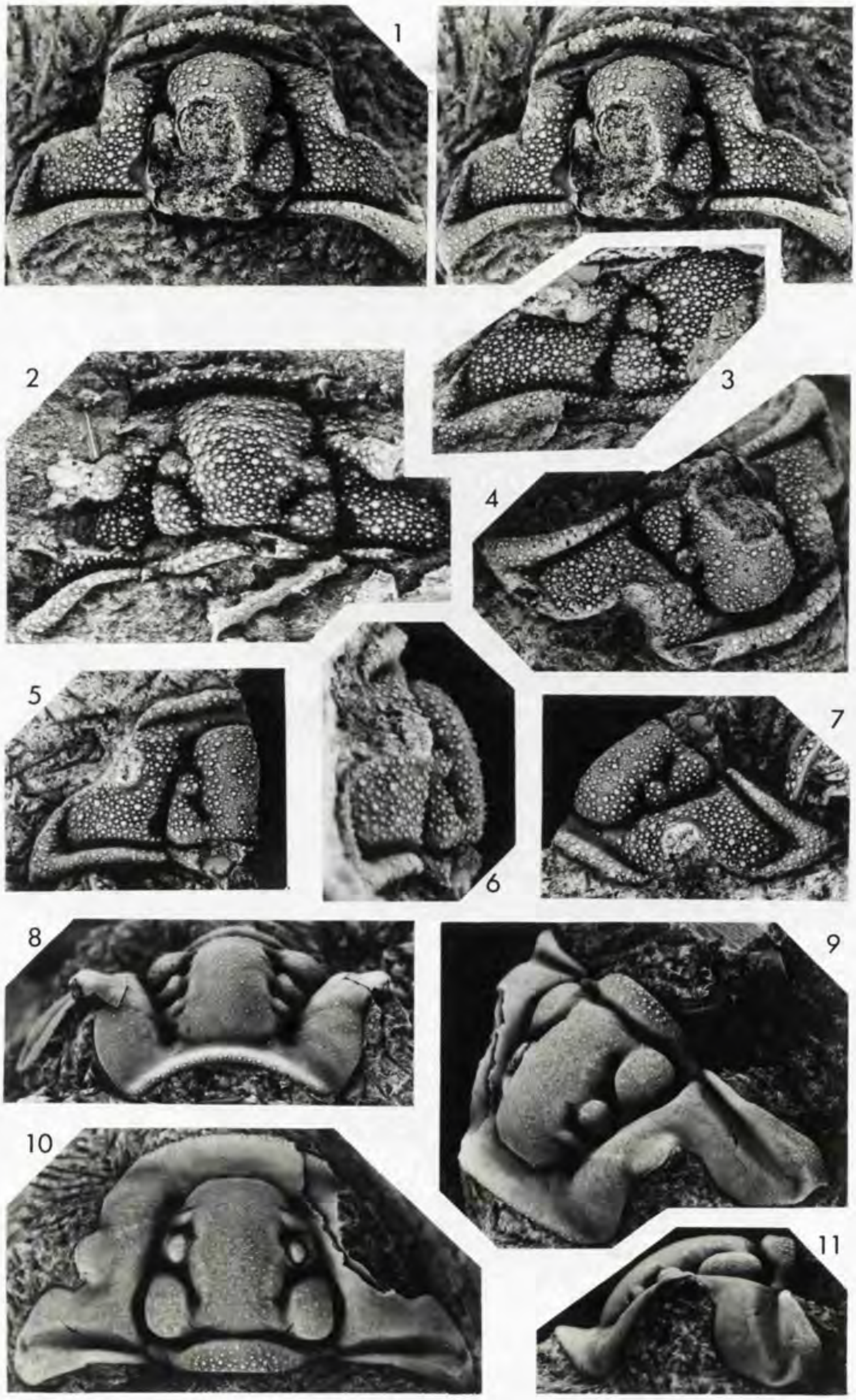

PLATE 4.

Figs. 1-9. Flexicalymene jemtlandica Thorslund, 1940

1-3, 6. Incomplete cranidium, PMO 91079, 1.8 metres below the top of the Upper Chasmops Limestone (4b δ), N Raudskjaer, Oslo-Asker district. Coll. F. Nikolaisen, 9. 9. 1968. Dorsal, frontal, right oblique stereo-pairs, right lateral view, x 4. See also Pl. 5, fig. 11.

4, 8, 9. Incomplete cranidium, PMO 81112/9/2, 1.8 metres under the top of the Upper Chasmops Limestone (4b δ), N Raudskjaer, Oslo-Asker district. Right lateral, right oblique views, dorsal stereo-pair, x 4. See also Pl. 3, fig. 8.

5. Incomplete cranidium, PMO 81218, Upper Chasmops Limestone (4b δ), S Norderhov (Lok 2a), Ringerike district. Coll. L. Størmer, 1929. Dorsal view, x 3.

7. Incomplete cranidium, PMO 81067, Upper Chasmops Limestone (4b ζ), road profile, Norderhov, Ringerike district. Coll. G. Hamar. Dorsal view, x 3.

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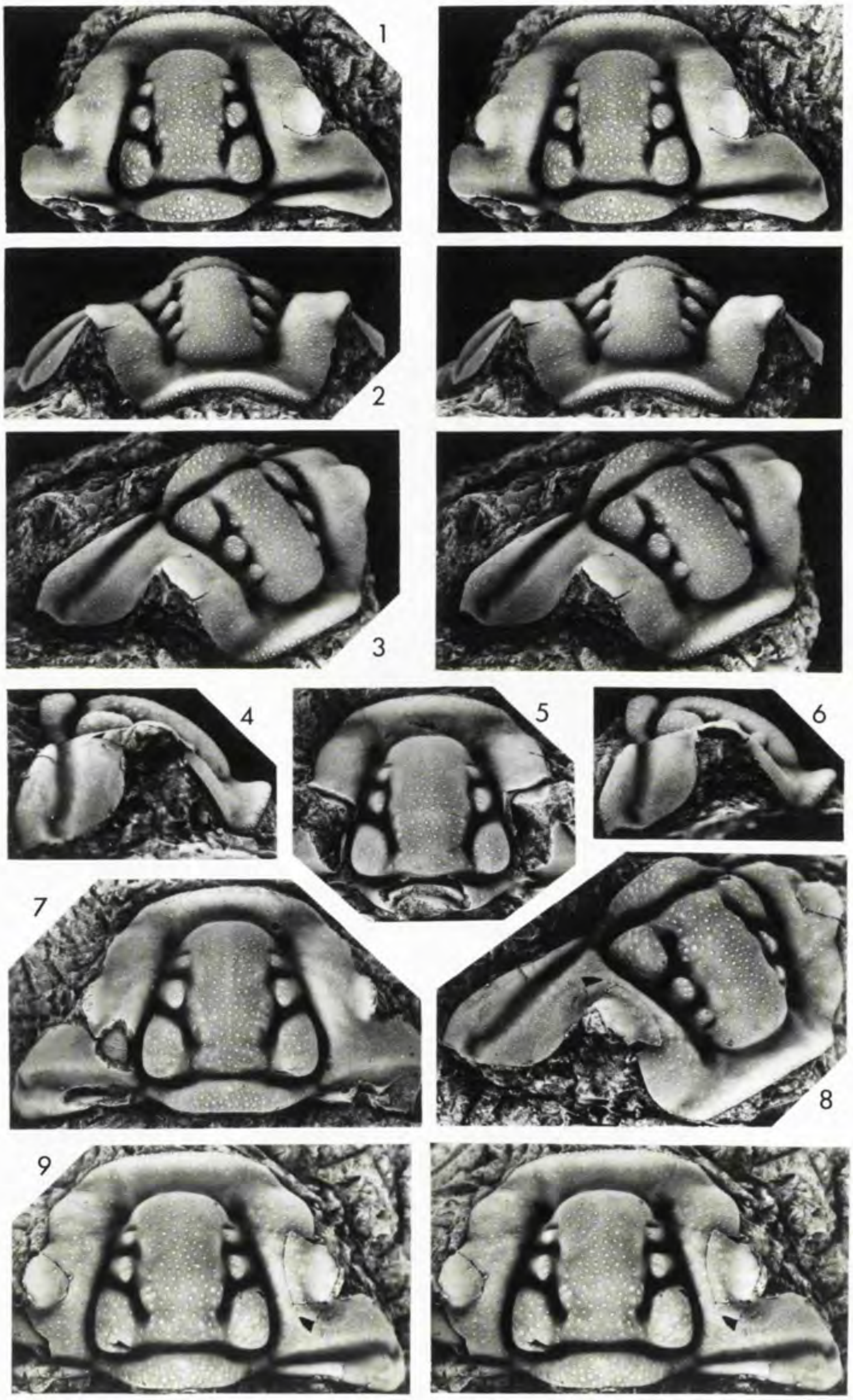

PLATE 5 (continued)

Fig. 10. *Flexicalymene scabustula* sp. nov.

Enlargement of part of glabella, PMO 81250, upper thick limestone bed, Upper *Chasmops* Limestone (4bδ), N Nakholmen, Inner Oslofiord, Oslo-Asker district. Coll. G. Henningsmoen, 29. 2. 1962. Dorsal view, x 10. See also Pl. 6, figs. 1-4.

PLATE 5

Figs. 1-9, 11. Flexicalymene jemtlandica Thorslund, 1940

1. Pygidium, PMO 81313, 1.7 metres below the top of the Upper Chasmops Limestone (4bδ), N Raudskjaer, Oslo-Asker district. Coll. Nikolaisen, Bruton, Hamar, 1967. Posterior stereo-pair, x 4.

2, 9. Hypostome, PMO 81105 (on same block as fig. 6), 1.8 metres below the top of the Upper Chasmops Limestone (4bδ), N Raudskjaer, Oslo-Asker district. Coll. F. Nikolaisen, 19. 9. 1968. Right lateral view, ventral stereo-pair, x 8.

3, 4. Pygidium, PMO 81109, same horizon, locality and collector as for figs. 2, 9. Right oblique, posterior views, x 4.

5. Pygidium, PMO 5575, a cut 2 metres below the top of the Upper Chasmops Limestone (4bδ), Terneholmen, Oslo-Asker district. Coll. J. Kiaer, 9. 10. 1921. Posterior view, x 12.

6. Right free cheek, PMO 81105 (on same block as figs. 2, 9), same horizon, locality and collector as for figs. 2, 9. 'Dorsal' view, x 6.

7. Hypostome, PMO 91084, same horizon, locality and collector as for fig. 5. Ventral view, x 12.

8. Rostral plate, PMO 5577, same horizon, locality and collector as for fig. 5. Ventral view (border sector), x 8.

11. Enlargement of part of glabella, PMO 91079, 1.8 metres below the top of the Upper Chasmops Limestone (4bδ), N Raudskjaer, Oslo-Asker district. Coll. F. Nikolaisen, 9. 9. 1968. Dorsal view, x 10. See also Pl. 4, figs. 1-3, 6.

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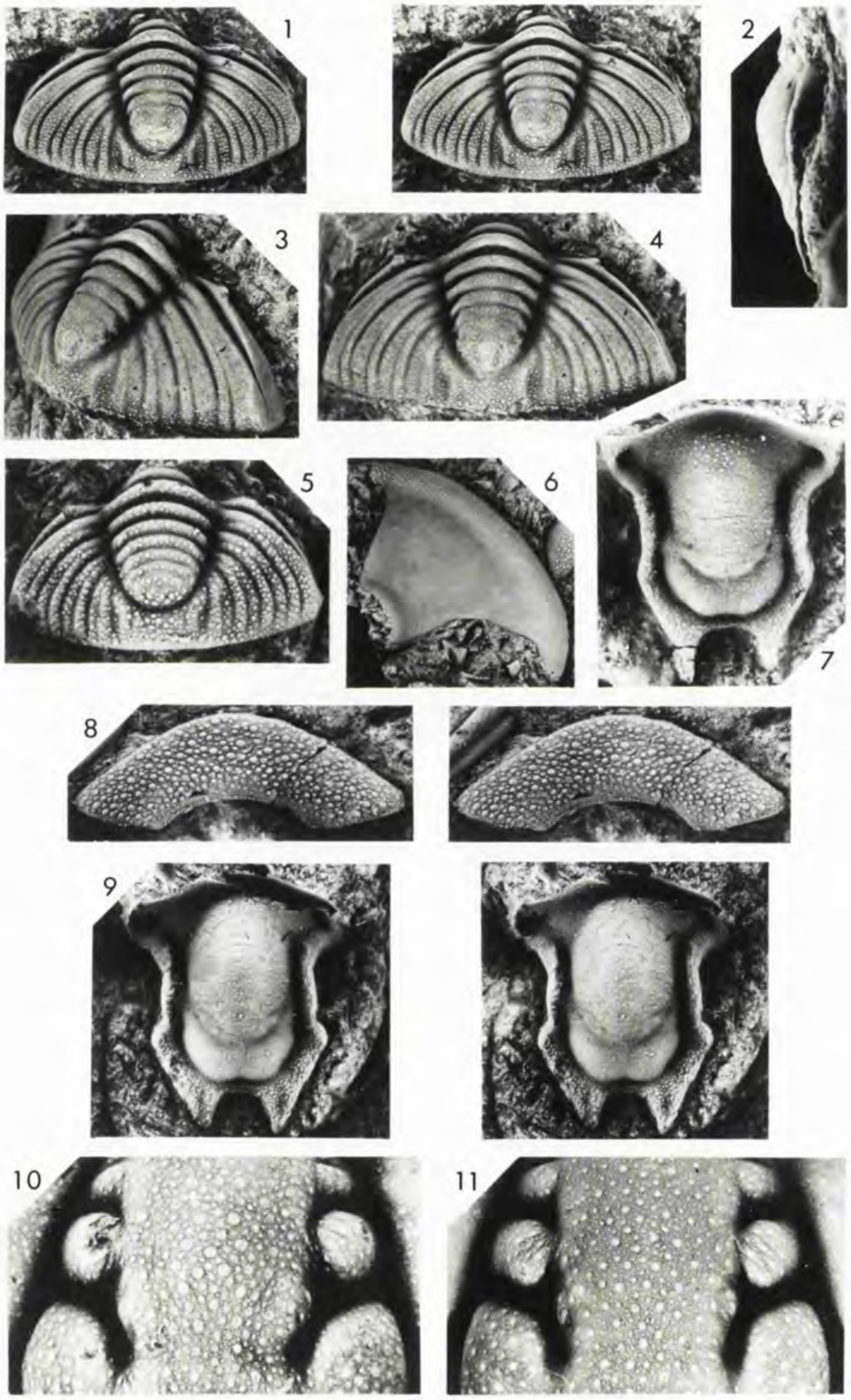

PLATE 6.

Figs. 1-9. Flexicalymene scabustula sp. nov.

1-4. Holotype, cranidium, PMO 81250, upper thick limestone bed, Upper Chasmops Limestone (4bδ), N Nakholmen, Inner Oslofiord, Oslo-Asker district. Coll. G. Henningsmoen, 29. 2. 1962. Dorsal, frontal, left oblique stereo pairs, left lateral view, x 4. See also Pl. 5, fig. 10.

5-8. Incomplete cranidium, PMO 81138, "Illaenus layer", Upper Chasmops Limestone (4bδ), Bygdøy - opposite Skarpsno, Oslo-Asker district. Coll. F. Nikolaisen, 6. 6. 1967. Frontal, right lateral, dorsal stereo-pair, right oblique views, x 4.

9. Cranidium, cuticle missing from most of glabella and part of fixed cheek, PMO 5491, uppermost limestone bench, Upper Chasmops Limestone (4bδ), Nakholmen, Inner Oslofiord, Oslo-Asker district. Coll. J. Kiaer, 8. 10. 1927. Dorsal view, x 3.

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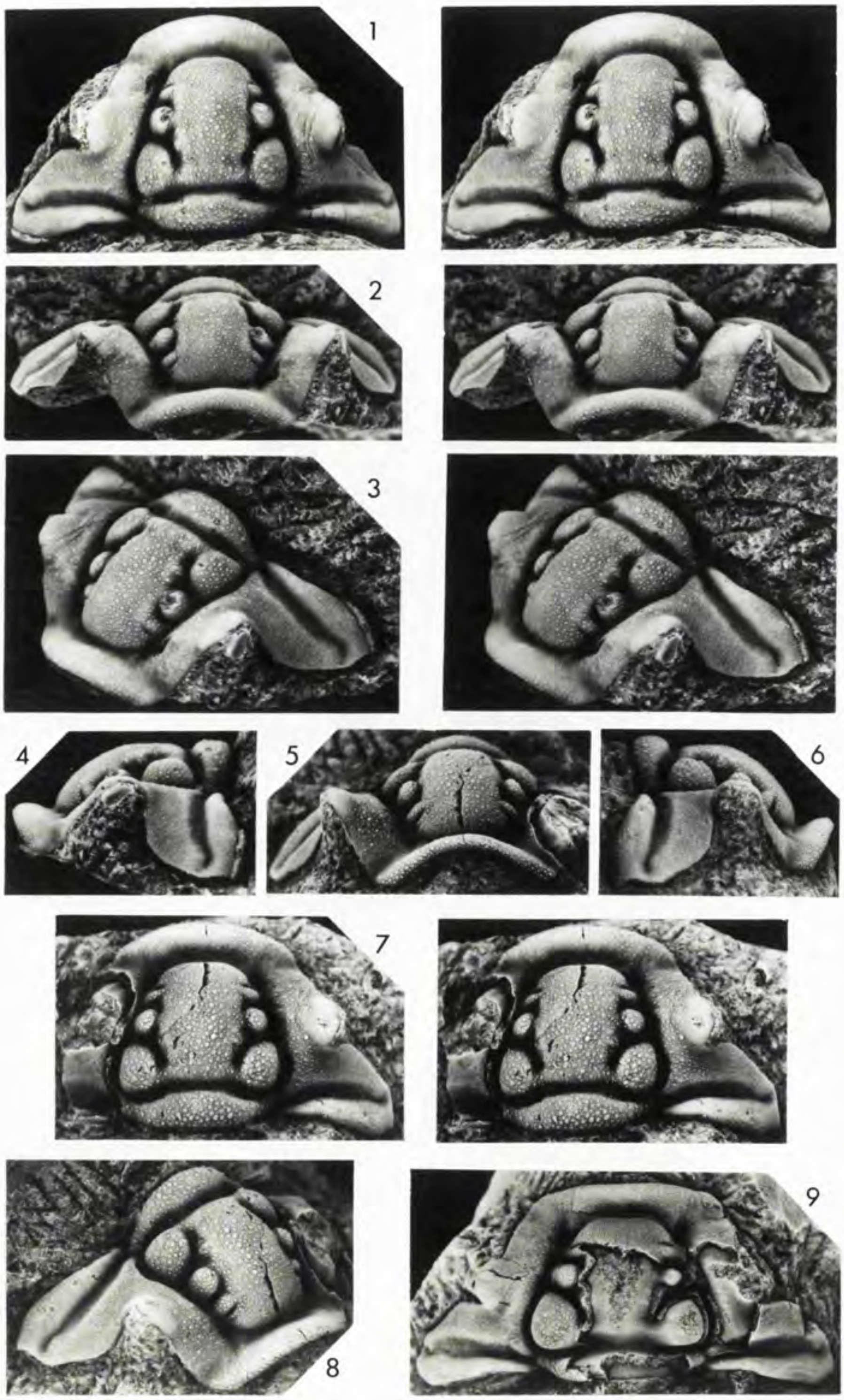

PLATE 7

Figs. 1-15. Flexicalymene scabustula sp. nov.

1, 2. Incomplete cranidium, PMO 81135, "Illaenus layer", Upper Chasmops Limestone (4bδ), Bygdøy - opposite Skarpsno, Oslo-Asker district. Coll. F. Nikolaisen, 6. 6. 1967. Dorsal, left lateral views, x 5.

3, 5. Isolated thoracic segment, PMO 81188, Upper Chasmops Limestone (4bδ), W side of Nakholmen, Inner Oslofiord, Oslo-Asker district. Right lateral, dorsal views, x 4.

4. Incomplete cranidium, PMO 91086, upper thick limestone bed, Upper Chasmops Limestone (4bδ), N Nakholmen, Inner Oslofiord, Oslo-Asker district. (Type locality). Coll. G. Henningsmoen, 29. 9. 1962. Dorsal view, x 4.

6. Rostral plate, PMO 91092, same horizon, locality and collector as for fig. 4. Ventral view (border sector), x 8.

7, 10, 11. Pygidium, PMO 81256, same horizon, locality and collector as for fig. 4. Left lateral view, posterior stereo-pair, dorsal view, x 4.

8, 9. Hypostome, PMO 91093, same horizon, locality and collector as for fig. 4. Ventral stereo-pair, left lateral view, x 7.

12. Left free cheek, PMO 81499, thick limestone bed, 6 metres below Lower Tretaspis Shale (4cα), Upper Chasmops Limestone, Land Steilene, S end of Island, Oslofiord, Oslo-Asker district. 'Dorsal' view, x 3.

13, 14. Pygidium, PMO 81500, same horizon, locality and collector as for fig. 12. Posterior, right oblique views, x 4.

15. Pygidium, PMO 5380, Upper Chasmops Limestone (4bδ), Rambergøya, Inner Oslofiord, Oslo-Asker district. Coll. 1921. Posterior view, x 12.

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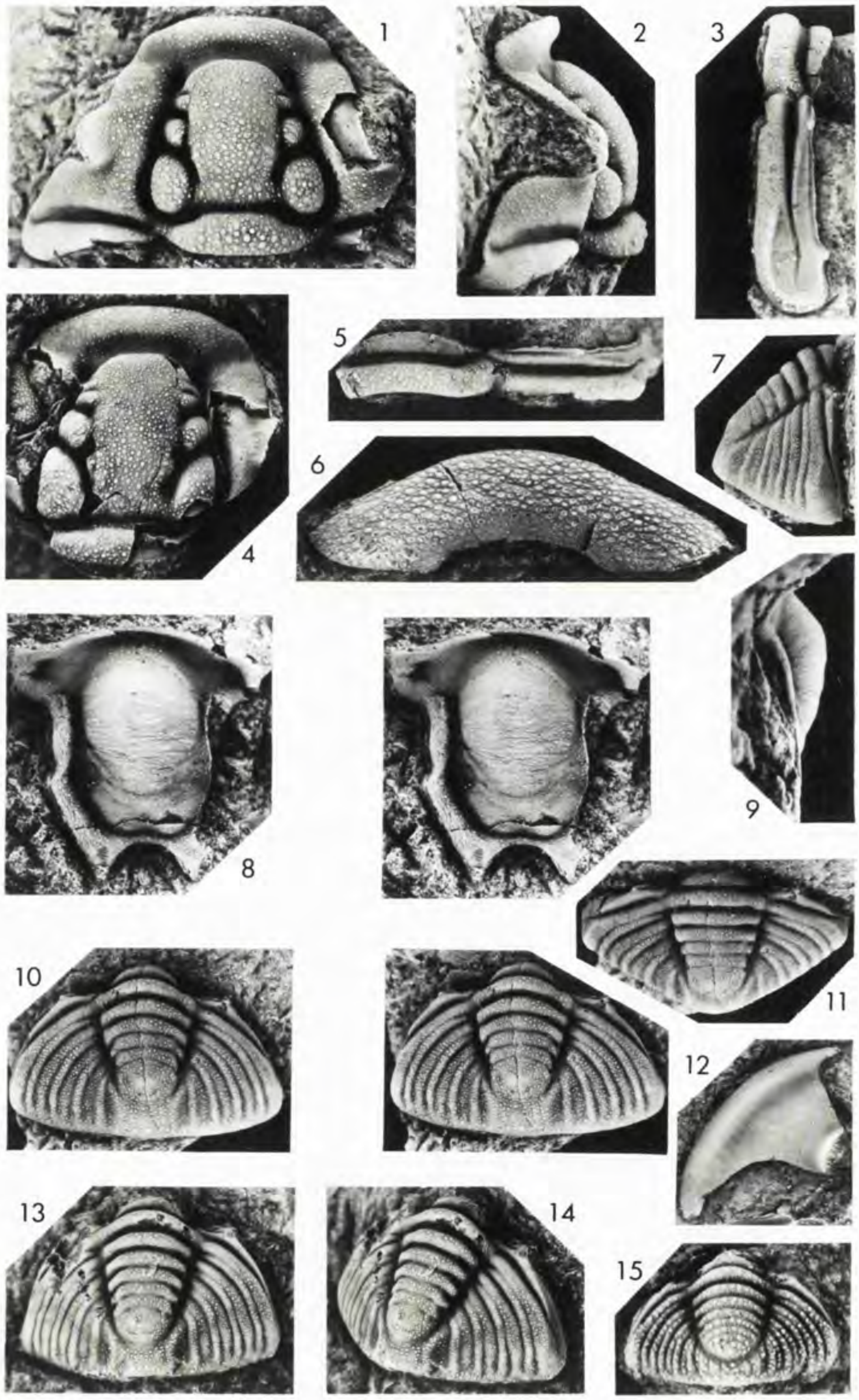

PLATE 8 (continued)

Fig. 10. Flexicalymene cf. F. scabustula sp. nov.

Incomplete cranidium, PMO 20399, Lower Chasmops Limestone (4bβ), NW Lindøya, Oslofiord, Oslo-Asker district. Coll. 24. 9. 1903. Dorsal view, x 4.

Fig. 12. Flexicalymene sp. indet. 2

Internal mould cranidium, PMO 91011, Upper Chasmops Shale (4bγ), N Hvalstad, Oslo-Asker district. Coll. N. Spjeldnaes, 1950. Dorsal view, x 3.

Fig. 13. Flexicalymene sp. indet. 3

Incomplete cranidium, PMO 61521, Upper Chasmops Shale (4bγ), Hestesund, Landøya, Oslo-Asker district. Coll. J.F. Bockelie, & F. Nikolaisen, 31. 5. 1966. Dorsal view, x 3.

PLATE 8

Figs. 1-4. Flexicalymene (Reacalymene) sp. nov.

Incomplete cranidium, cuticle missing from most of glabella, PMO 69372, 0-1 metre in the profile, Upper Chasmops Limestone (4bδ), Ballangrud, Hadeland district. Coll. L. Størmer. Dorsal stereo-pair, left lateral, left oblique, frontal views, x 3.

Figs. 5, 7. Flexicalymene cf. F. caractaci (Salter, 1865)

Internal mould cranidium, PMO 8173, Lower Chasmops Shale (4bα), small quarry S of 143 Ringsaas, Ringerike district. Coll. J. Kiaer, 31. 8. 1923. Dorsal view, x 3; right lateral view, x 4.

Figs. 6, 8, 9, 11. Flexicalymene sp. indet. 1

6. Internal mould pygidium, PMO 81679, Lower Chasmops Shale (4bα), N Hvalstad, Oslo-Asker district. Coll. N. Spjeldnaes, 4. 9. 1950. Posterior view, x 4.

8. 'Silcoset' rubber cast of external mould cranidium, PMO 81678, same horizon, locality and collector as for fig. 6. Dorsal view, x 3.

9, 11. 'Silcoset' rubber cast of external mould cranidium, PMO 81641, Lower Chasmops Shale (4bα), Blomenholm, Baerum, Oslo-Asker district. Coll. P. Wendilbo, 13. 4. 1952. Right oblique, dorsal views, x 3.

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PLATE 9

Figs. 1-8. *Gravicalymene capitovata* sp. nov.

1-4, Holotype, 'Silcoset' rubber cast of external mould
6-8. cranidium, PMO 91061, internal mould cranidium, PMO 91062, *Ogygiocaris* Shale ($4a\alpha_3$), loose block from the scree at the road cutting, Muggerudkleiva, Eiker-Sandsvaer district. Coll. D.L. Bruton, 8. 6. 1971. Dorsal, frontal stereo-pairs, right oblique, right lateral view, x 2.5; dorsal, frontal, left oblique views, x 3.

5. 'Silcoset' rubber cast of external mould cranidium, PMO 91045, same horizon and locality as for figs. 1-4, 6-8. Coll. D.L. Bruton, & D.J. Siveter, 1971. Dorsal view, x 2.

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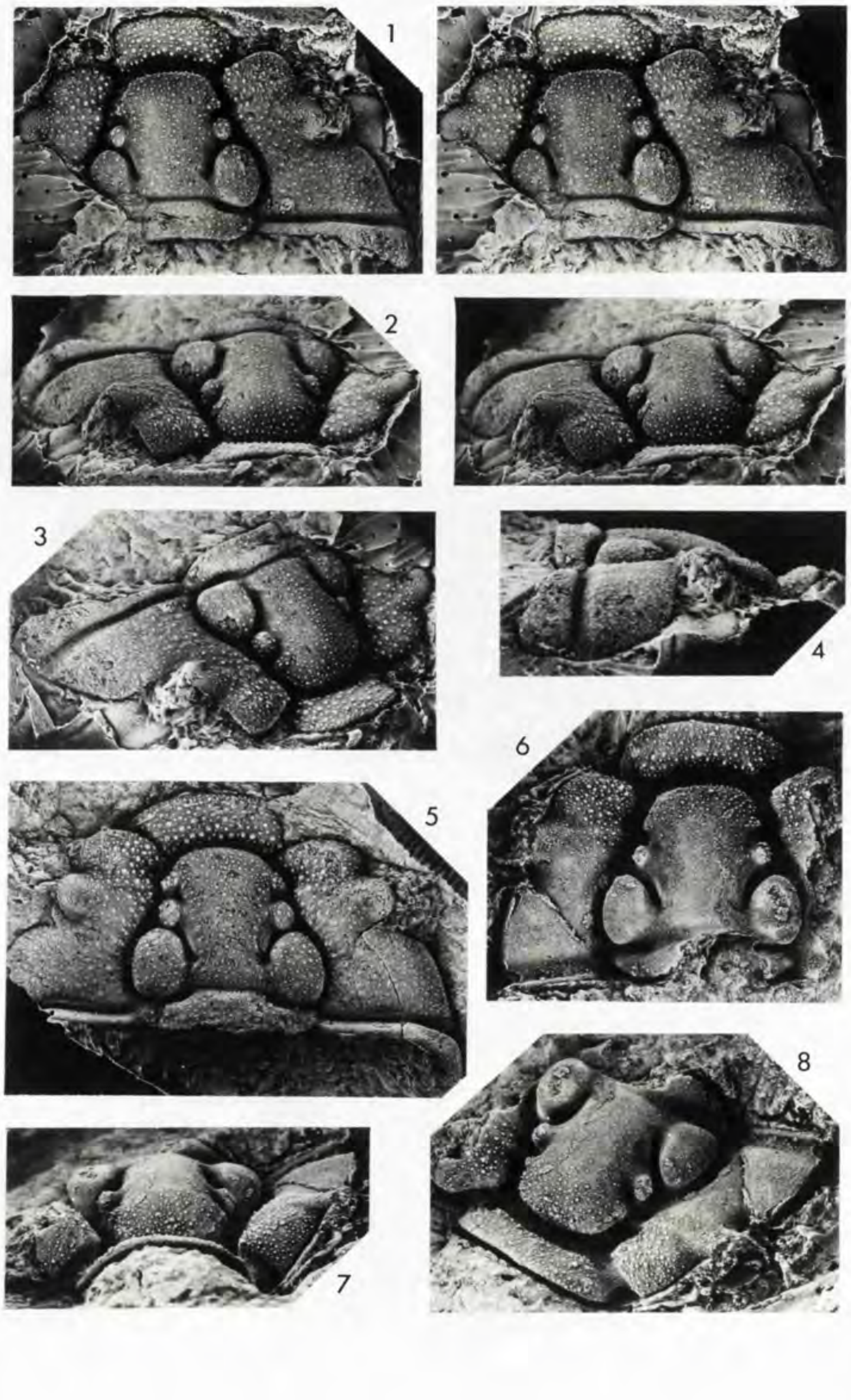

PLATE 10 (continued)

Figs. 2, 3, 10. *Quadricalymene lirella* gen. *et* sp. nov.

2. 'Silcoset' rubber cast of external mould cranidium, PMO 91071, *Ogygiocaris* beds ($4a\alpha_{3-4}$), Muggerudkleiva, Eiker-Sandsvaer district. Coll. N. Spjeldnaes, 1961. Dorsal view, x 6.

3, 10. Internal mould of almost complete specimen, PMO 91065, same horizon, locality and collector as for fig. 2. Posterior view of pygidium (underturned), x 5; dorsal view, x 3.

Fig. 4. *Gravicalymene* aff. *G. capitovata* sp. nov.

'Silcoset' rubber cast of external mould cranidium, PMO 81575, from "the Shales" (Lower *Chasmops* Shale ?), the 'new' road, 30-50m N of Montebello station, Ullern, Oslo district. Coll. J.A. Dons, 1944. Dorsal view, x 3.

PLATE 10

Figs. 1, 5-9, 11, 12. *Gravicalymene capitovata* sp. nov.

1. 'Silcoset' rubber cast of external mould pygidium, PMO 60410, *Ogygiocaris* Shale ($4a\alpha_{3-4}$), Muggerudkleiva, Eiker-Sandsvaer district. Coll. L. Størmer, 1925-27. Posterior view, x 2.

5. Internal mould cranidium, PMO 82681, *Ogygiocaris* Shale ($4a\alpha_{3-4}$), Muggerudkleiva, Eiker-Sandsvaer district. Coll. 16. 5. 1965. Dorsal view, x 1.5.

6, 9. Internal mould pygidium, PMO 91061 (on the same block and positioned next to holotype cranidium), *Ogygiocaris* Shale ($4a\alpha_3$), loose block from the scree at Muggerudkleiva, Eiker-Sandsvaer district. Coll. D.L. Bruton, 8. 6. 1971. Posterior stereo-pair, left oblique view, x 2.5.

7. 'Silcoset' rubber cast of external mould rostral plate, PMO 91036, same horizon and locality as for figs. 6, 9. Coll. D.L. Bruton, & D.J. Siveter, 1971. Ventral stereo-pair (border sector), x 3.5.

8. Internal moulds of two cranidia, PMO 66598, ? Upper *Didymograptus* Shale ($4a\alpha_{1-2}$), 24.50 metres from the bottom of profile, waterfall in Ravalsjøriver, Flatla, Hedenstad, Øvre Sandsvaer. Dorsal view, x 1.5. These two cranidia possibly represent those referred to by Størmer 1953, p. 79.

11. Internal mould free cheek, PMO 91063, same horizon, locality and collector as for fig. 1. 'Dorsal' view, x 2.5.

12. 'Silcoset' rubber cast of external mould hypostome, PMO 91051, same horizon and locality as for figs. 6, 9. Coll. D.L. Bruton, & D.J. Siveter, 1971. Ventral stereo-pair, x 3.5

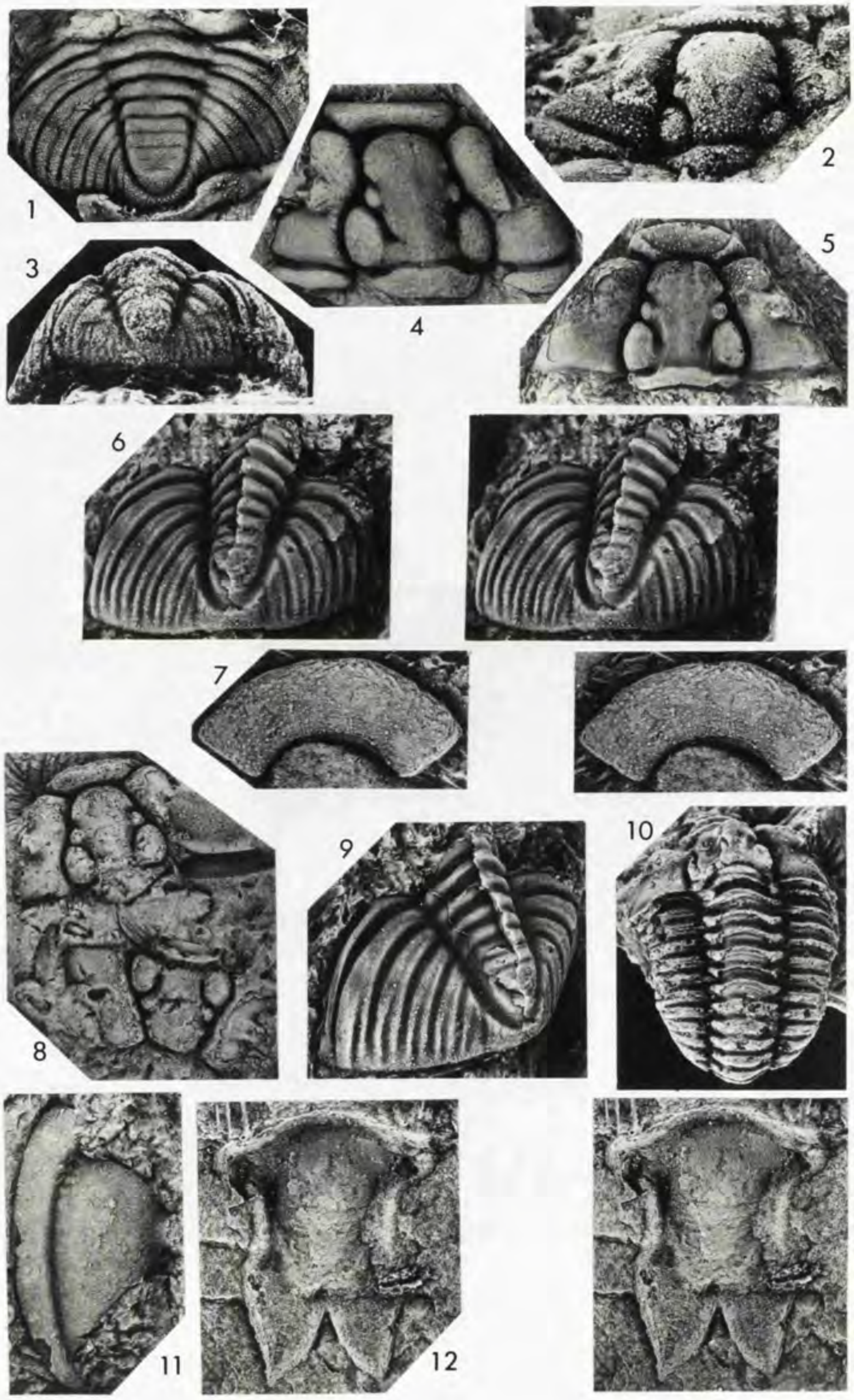
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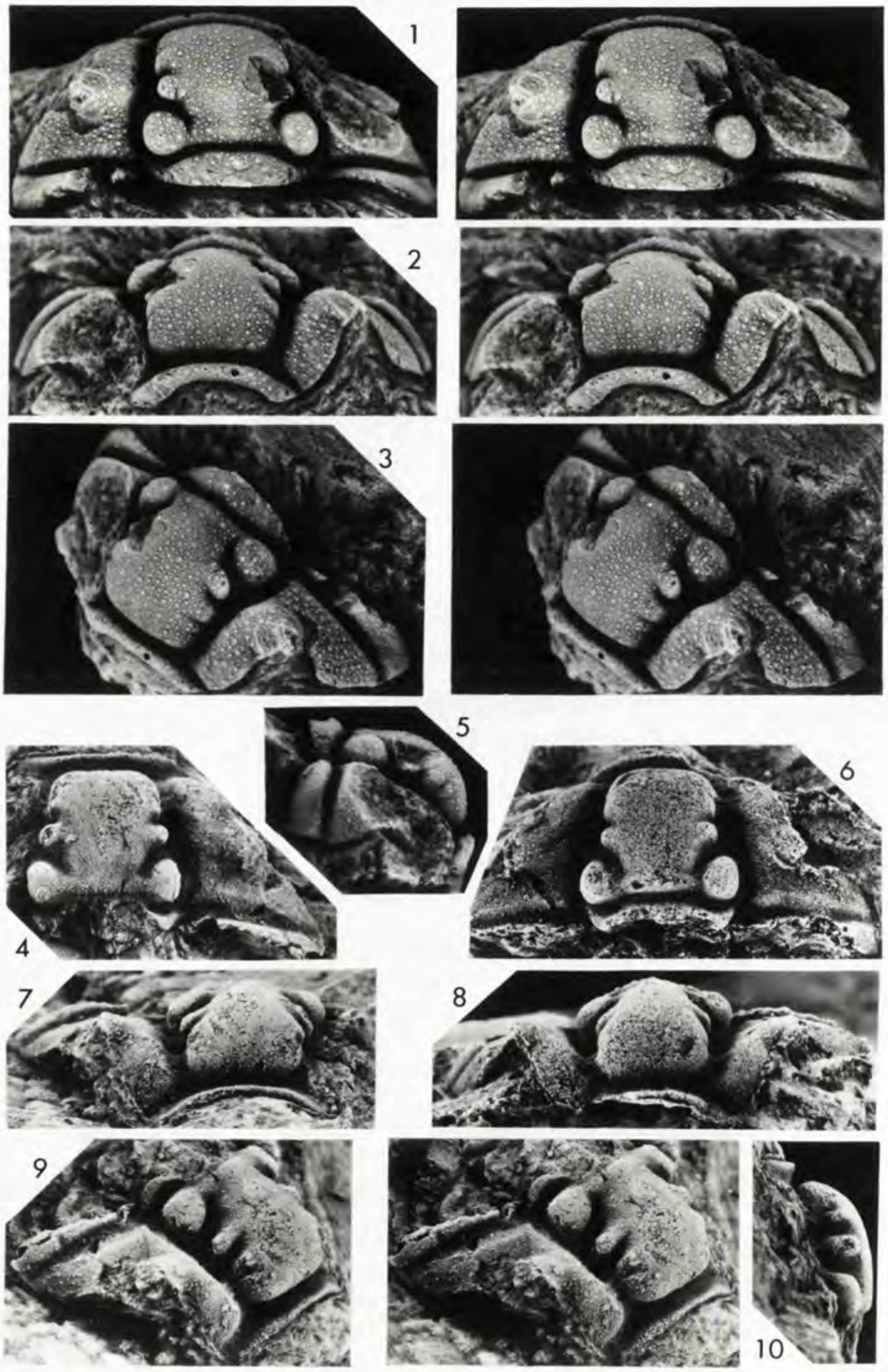
PLATE 11

Figs. 1-10. Quadricalymene lirella gen. et sp. nov.

1-3, 5. Holotype, incomplete cranidium, PMO 81919, Ampyx Limestone ($4a\beta$), W side of Bygdøy, Oslo-Asker district. Coll. F. Nikolaisen, 16. 4. 1961. Dorsal, frontal, left oblique stereo-pairs, right lateral view x 7.

4, 7, 9, 10. Internal mould cranidium, PMO 82466, Ogygiocaris beds ($4a\alpha_{3-4}$), Muggerudkleiva, Eiker-Sandsvaer district. Coll. N. Spjeldnaes, 1961. Dorsal, frontal views, right oblique stereo-pair, left lateral view, x 4.5.

6, 8. Internal mould cranidium, PMO 91072, same horizon, locality and collector as for figs. 4, 7, 9, 10. Dorsal, frontal views, x 4.5.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CHAPTER C PLATES 1-3

METACALYMENE KEGEL, 1927, A MONOTYPIC CALYMENID FROM THE KOPANINA FORMATION (SILURIAN) OF BOHEMIA.

PLATE 1

Figs. 1-3, 6, 8. Metacalymene baylei (Barrande, 1846)

1, 2, 6. Incomplete cranidium, DJS/125, Kopanina Formation, Kosov, Bohemia. Coll. D.J. Siveter & L. Marek, 1971. Dorsal stereo-pair, left lateral, frontal views, x 6.

3. Cast of internal mould of almost complete specimen, NMP It879, CE1253, Kopanina Formation (horizon with Cromus beaumonti), Jarov (Dlouha hora), Bohemia. Dorsal stereo-pair, x 1.5. Figured Barrande 1852, pl. 43, figs. 49, 50. See also Pl. 2, figs. 1, 7, 8.

8. Syntype ?, cast of internal mould cranidium, NMP 624/66, Kopanina Formation, Kolednik, Bohemia. Dorsal view, x 4.

Figs. 4, 5, 7. Metacalymene baylei? (Barrande, 1846)

Incomplete hypostome, DJS/127a, b, Kopanina Formation, Kosov, Bohemia. Coll. D.J. Siveter & L. Marek, 1971. 'Silcoset' rubber cast of external mould, DJS/127b, left lateral view, x 8, ventral stereo-pair, x 6; ventral stereo-pair, DJS/127a, x 6.

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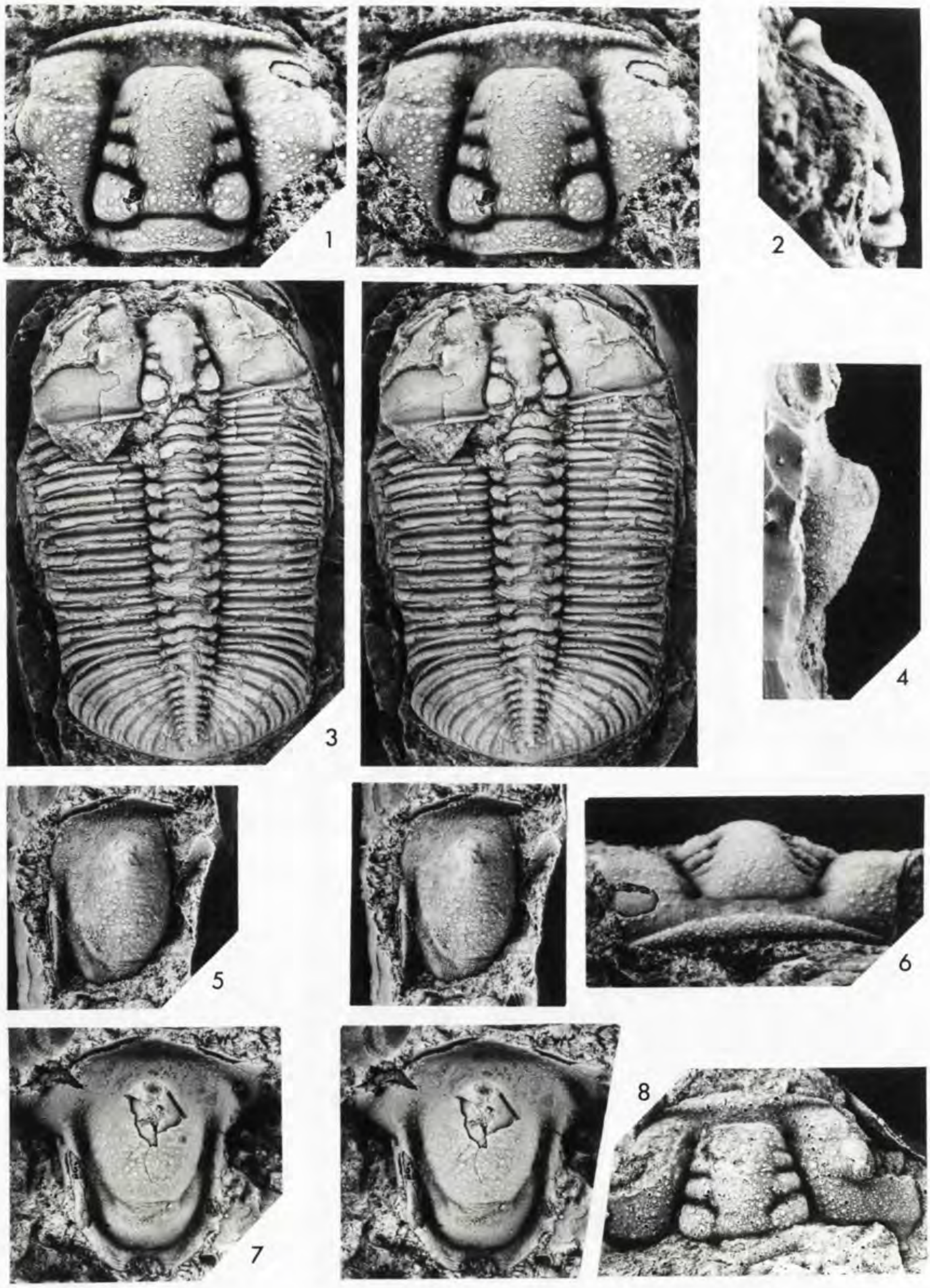

PLATE 2

Figs. 1-5, 7, 8. Metacalymene baylei (Barrande, 1846)

1, 7, 8. Cast of complete specimen of which much of the cuticle is missing, NMP It880, CE1255, Kopanina Formation (horizon with Cromus beaumonti), Ohrada (=Reporyje, Muslovka), Bohemia. Dorsal stereo-pair, dorsal, right oblique views, x 2. Additional specimen used by Barrande (1852) for the completion of his pl. 43, figs. 49, 50. See also Pl. 1, fig. 3.

2-5. 'Silcoset' rubber cast of external mould cranidium, DJS/128, Kopanina Formation, Kosov, Bohemia. Coll. D.J. Siveter & L. Marek, 1971. Left lateral view, x 5; dorsal stereo-pair, right oblique, frontal views, x 3.5.

Fig. 6. Metacalymene baylei? (Barrande, 1846)

Cast of internal mould hypostome, NMP It 881, Kopanina Formation (horizon with Cromus beaumonti, Jarov (Dlouha hora), Bohemia. Ventral view, x 6. Figured Barrande 1852, pl. 43, figs. 51, 52.

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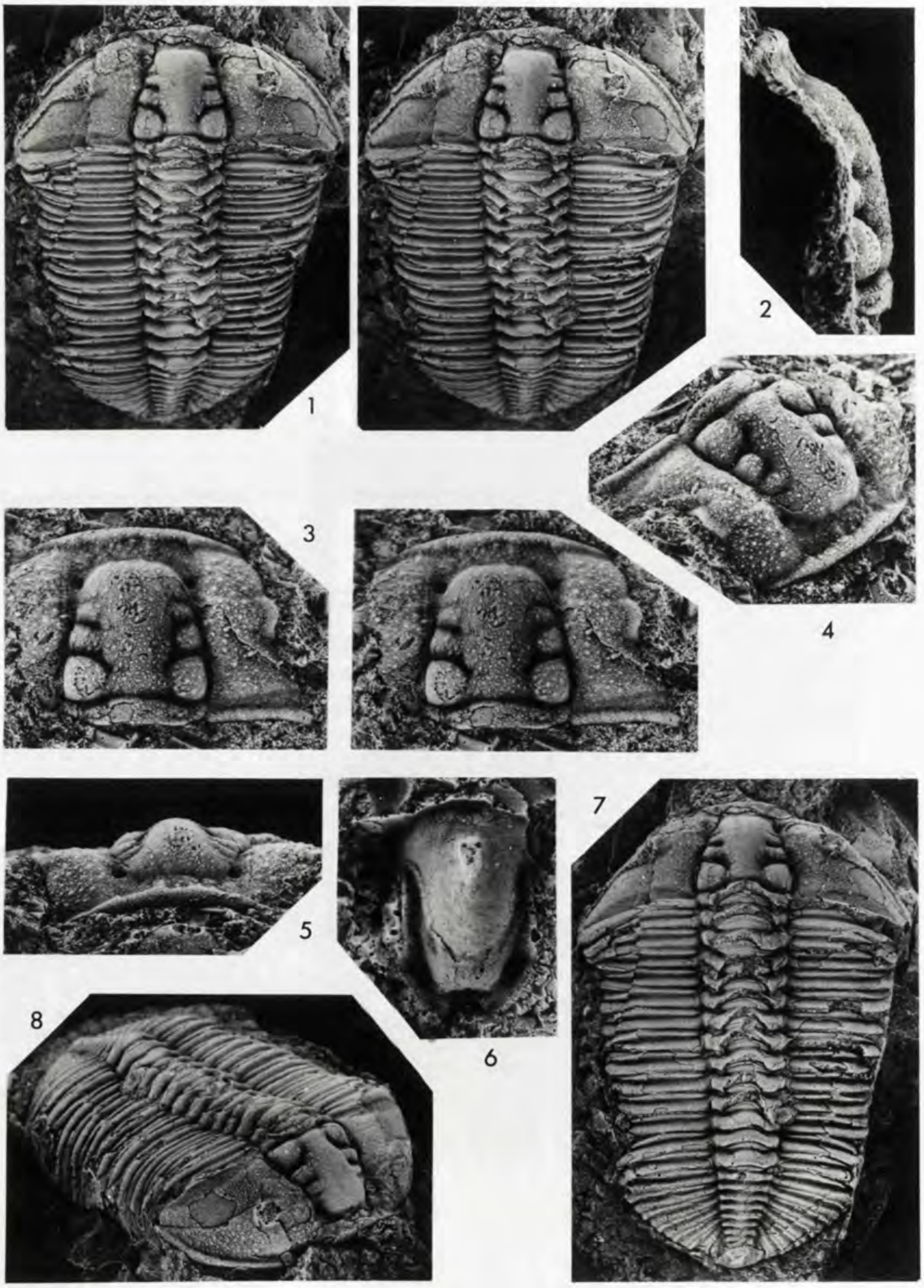


PLATE 3

Figs. 1-9. Metacalymene baylei (Barrande, 1846)

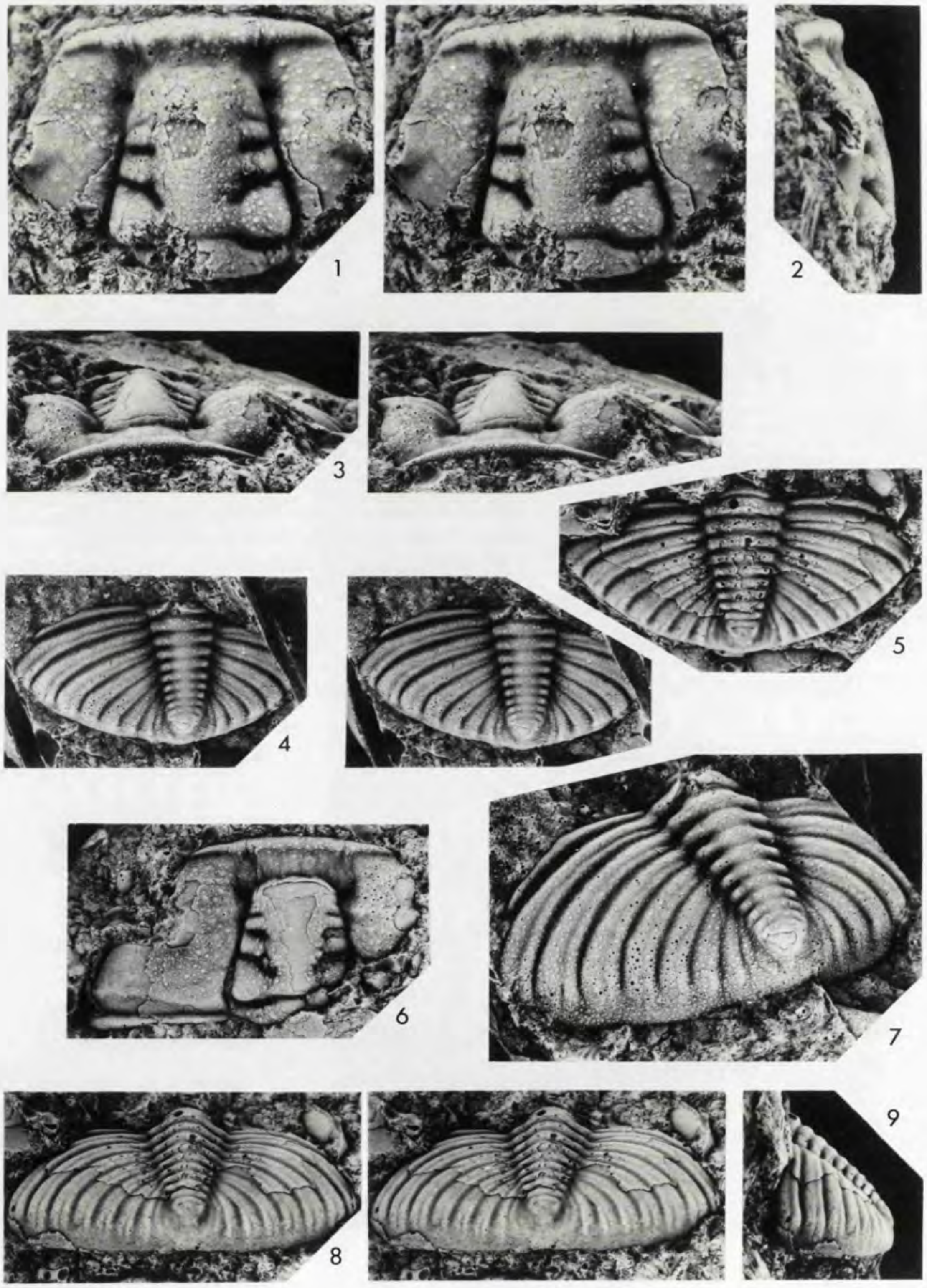
1, 2. Incomplete cranidium, DJS/126, Kopanina Formation, Kosov, Bohemia. Coll. D.J. Siveter & L. Marek, 1971. Dorsal stereo-pair, left lateral view, x 6.

3, 6. Cast of incomplete cranidium, NMP It348, Kopanina Formation (horizon with Cromus beaumonti), Jarov (Dlouha hora), Bohemia. Frontal stereo-pair, dorsal view, x 2.5. Figured Barrande 1852, pl. 19, fig. 28.

4, 7. Cast of incomplete pygidium, NMP It349, Kopania Formation (horizon with Cromus beaumonti), ? Reporyje, Bohemia. Dorsal stereo-pair, x 2.5; left oblique view, x 4. Additional specimen used by Barrande (1852) for the completion of his pl. 19, fig. 29. See also Pl. 3, figs. 5, 8, 9.

5, 8, 9. Cast of pygidium, NMP It349 (same number as previous specimen), Kopanina Formation (horizon with Cromus beaumonti), Jarov (Dlouha hora), Bohemia. Dorsal view, posterior stereo-pair, left lateral view, x 3. Figured Barrande 1852, pl. 19, fig. 29. See also Pl. 3, figs. 4, 7.

3



CHAPTER D PLATES 1-14

THE GENUS *DIACALYMENE* KEGEL, 1927 FROM THE UPPER ORDOVICIAN AND SILURIAN OF BRITAIN, SCANDINAVIA, AND CZECHOSLOVAKIA.

PLATE 1 (continued)

Fig. 9. Diacalymene sp. indet.

Incomplete poorly preserved cranidium, internal mould, PMO 91114, upper Tretaspis Series, Stage 5a, Ovre Nes badestrand, Oslo-Asker district, Oslo Region, Norway. Coll. J.F. Bockelie, 1964. Dorsal view, x 2½.

PLATE 1

Figs. 1-8, 10, 11. Diacalymene marginata Shirley 1936.

1. Incomplete cranidium, partially exfoliated, PMO 10112, highest part of Tretaspis Shale (4c), Frognoens south-west spids, Ringerike district, Oslo Region, Norway. Coll. J. Kiaer, 1917. Dorsal stereo-pair, x 4.

2, 4, 5. Incomplete cranidium, internal mould, PMO 65192, upper part of Lower Tretaspis Shale, railroad section near Bekkeli, S of Lunnar, Hadeland district, Oslo Region, Norway. Coll. L. Størmer, 1945. Left lateral, frontal views, x 2½; dorsal view, x 2. Holotype of Reacalymene (?) holtedahli Størmer, 1945, p. 415, pl. 2, fig. 7.

3, 10, 11. Incomplete pygidium, PMO 10106, Tretaspis Shale (4c), Frognoens west spids, Ringerike district, Oslo Region, Norway. Coll. J. Kiaer, 1915. Dorsal stereo-pair, posterior view, x 2½; left oblique view, x 4.

6. Incomplete cranidium, PMO 65195, same horizon, locality and collector as for fig. 2. Dorsal view, x 2½. Figured Størmer 1945, pl. 2, fig. 6 as Reacalymene (?) holtedahli n.sp.

7, 8. Incomplete pygidium, PMO 35068, same horizon and locality as for fig. 2. Coll. O. Holtedahl, 1914. Dorsal, posterior views, x 2½. Figured Størmer 1945, pl. 2, fig. 8. as Reacalymene (?) holtedahli n. sp.

Incomplete poorly preserved cranidium, internal mould, PMO 91114, upper Tretaspis Series, Stage 5a, Ovre Nes badestrand, Oslo-Asker district, Oslo Region, Norway. Coll. J.F. Bockelie, 1964. Dorsal view, x 2½.

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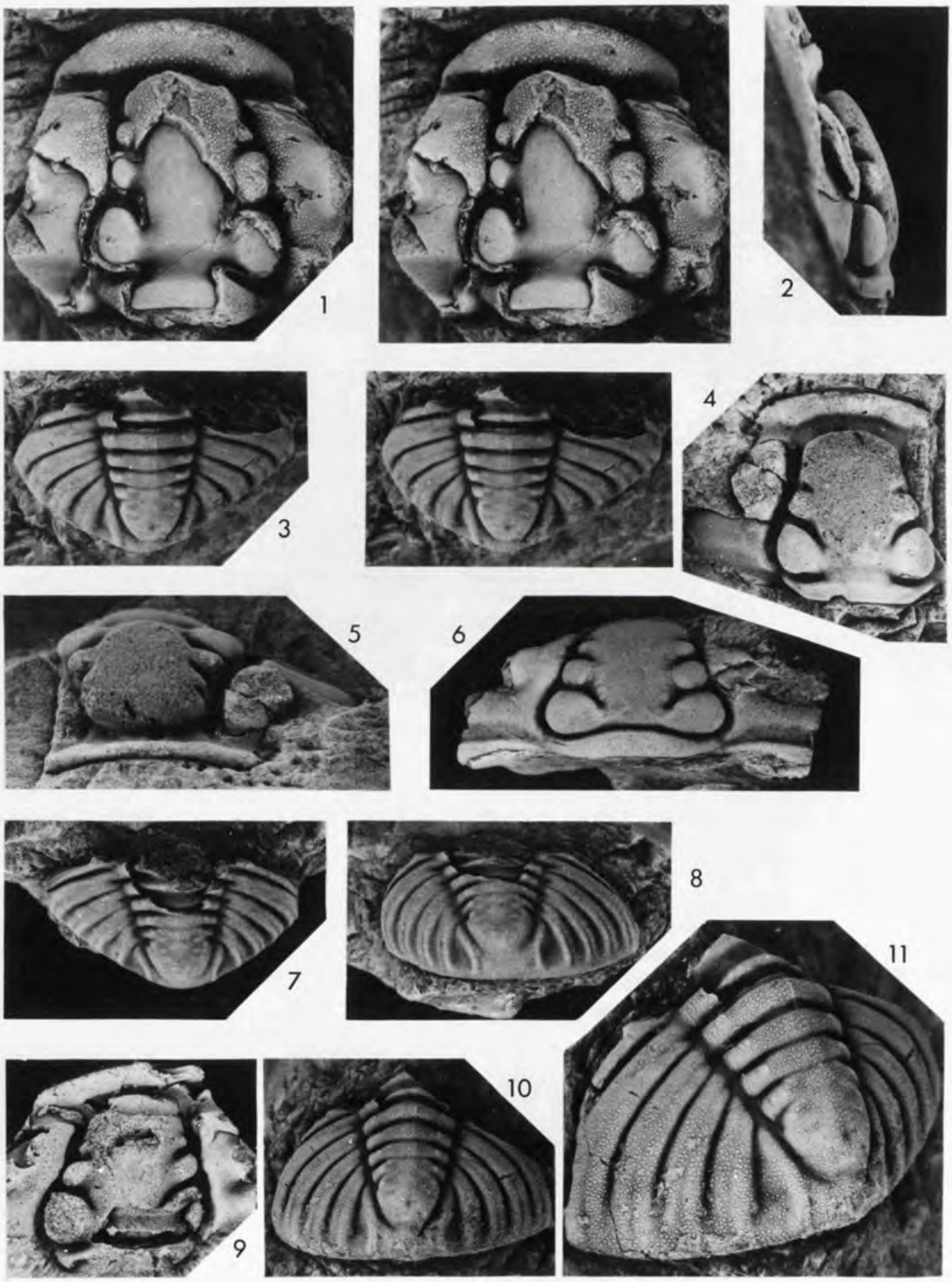

PLATE 2

Figs. 1-4, 6, 7, 9, 10, 11. Diacalymene marginata Shirley, 1936

1, 2. Incomplete cranidium, 'Silcoset' rubber cast of external mould (fig. 1) and internal mould (fig. 2), GSM 2120, GSM 2117, Ddolhir Beds, Ashgill Series, 800 yards S of the angle in the fence at summit of Moel Fferna, Denbighshire. Dorsal stereo-pair, dorsal view, x 3. Cited Shirley 1936, p. 416; Cave 1965, p. 295.

3, 4. Incomplete cranidium, internal mould, HM A1137a, Crinoid Bed, Lower Drummuck Group, Cautleyan Stage, Ashgill Series, Approximately 680 yards SW of High Mains Farmhouse, E brow of Quarrel Hill, Craighead - Glenshalloch Inlier, Girvan district. Loc. 5 of Lamont 1935, p. 300, pl. 9. Dorsal stereo-pair, frontal view, x 4. Cited Lamont 1935, p. 298 as Calymene sp.

6, 9. Incomplete cranidium, internal mould, BM In16851 (T. Ruddy colln.), Orthisina Zone, Cerig Coedog, S base of Moel Ferna, 6 m SE of Corwen, N Wales. Dorsal, right lateral views, x 2. Cited Shi ley 1936, p. 416.

7, 10, 11. Incomplete cranidium, plaster cast of internal mould, HM A941, Quarrel Hill Mudstones, Lower Drummuck Group, Cautleyan Stage, Ashgill Series, E brow of Quarrel Hill, Craighead - Glenshalloch Inlier, Girvan district. Loc. 4 of Lamont 1935, p. 300, pl. 9. Left oblique, right lateral views, dorsal stereo-pair, x 2½.

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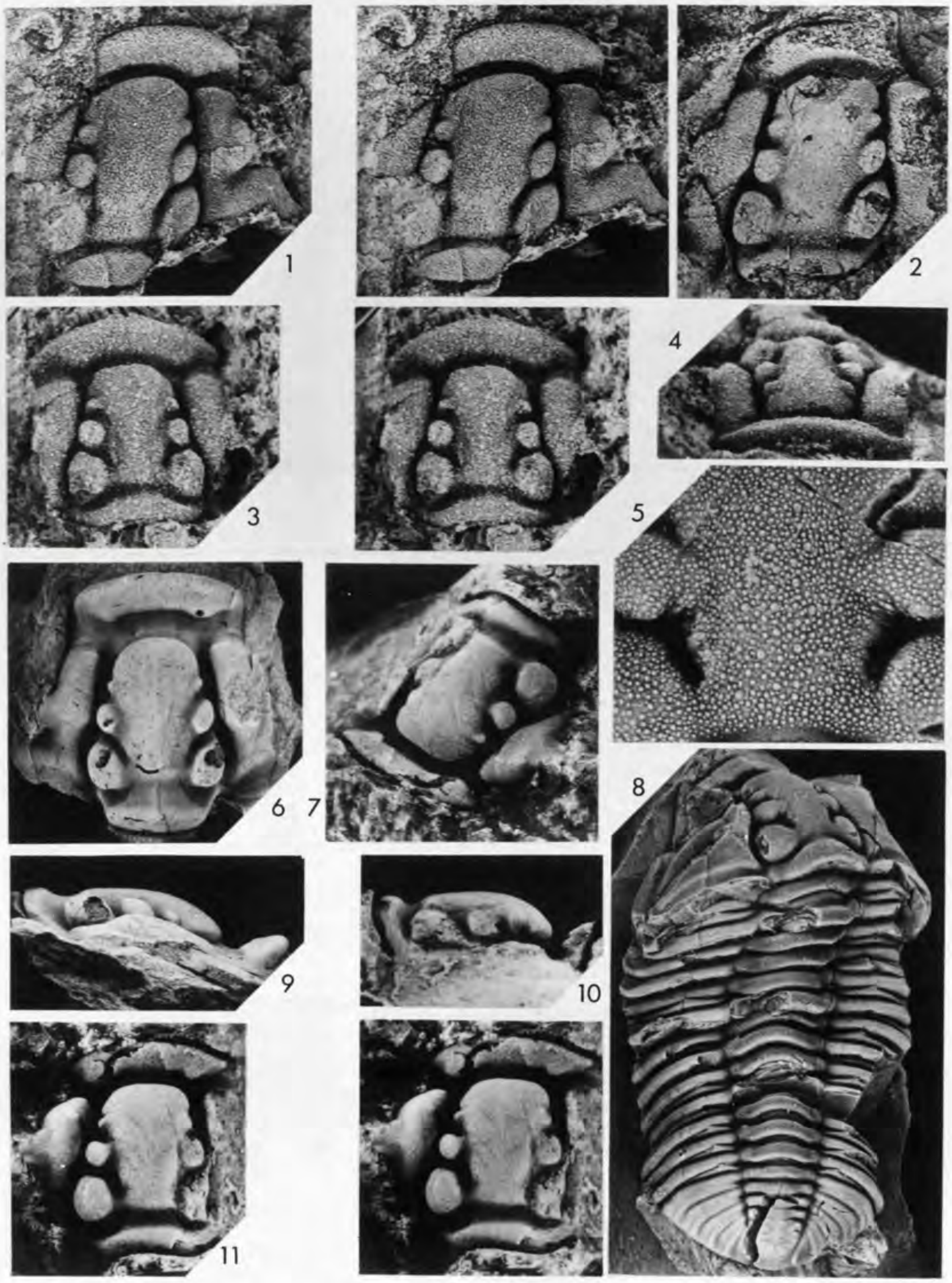

PLATE 3

Figs. 1-7. Diacalymene sp. B

1, 2, 4, 5. Almost complete specimen, IM Ar47706, Dalmanitina Beds, (Ashgillian in age) Kullsberg, Dalarna, Sweden. Dorsal stereo-pair, right lateral, right oblique, posterior views, x 3.

3, 6, 7. Almost complete specimen, SGU unnumbered, erratic of Östersjo Limestone (Ashgillian in age), N Baltic. Coll. Schmalensee, 1886. Right oblique view of pygidium, x 7; dorsal stereo-pair, left lateral view, x 2. Figured Wiman 1907, pl. 8, figs. 28, 32 as Calymene trinucleina. See also Pl. 2 , figs. 5, 8.

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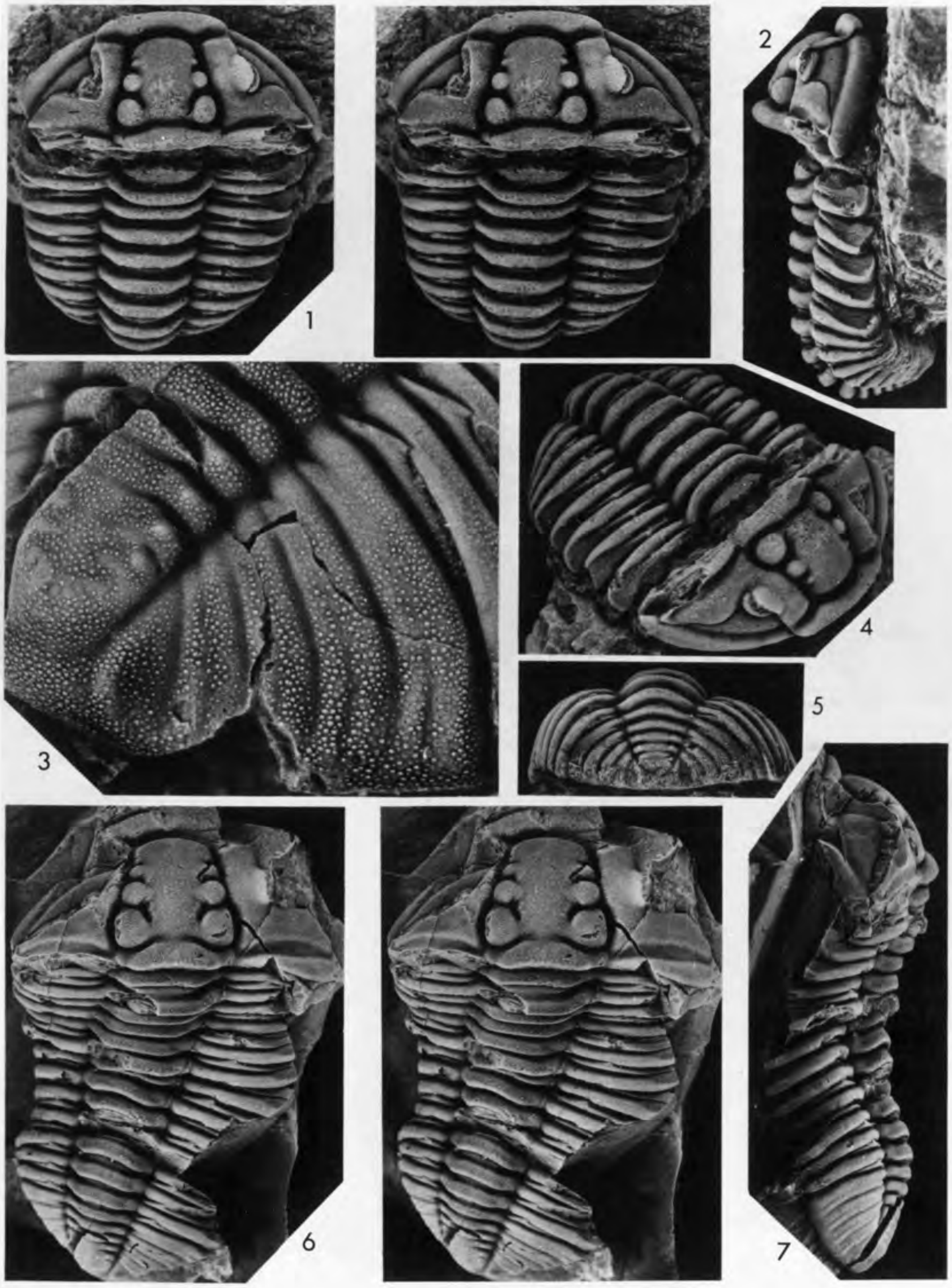

PLATE 4

Figs. 1-11. Diacalymene drummuckensis (Reed, 1906)

1-3, 5. Incomplete cranidium, partially exfoliated, WM unnumbered, Upper Drummuck Group, Rawtheyan Stage, Ashgill Series, Drummuck Burn, Girvan district. Dorsal stereo-pair, left lateral view, frontal, left oblique stereo-pairs, x $1\frac{1}{2}$.

4, 6. Incomplete hypostome, 'Silcoset' rubber cast of external mould, HM A910, Ladyburn mudstones, Upper Drummuck Group, Rawtheyan Stage, Ashgill Series. Lateral, ventral views, x $2\frac{1}{2}$.

7. Incomplete hypostome, 'Silcoset' rubber cast of external mould, HM A759a, Starfish Bed no. 2, Upper Drummuck Group, Rawtheyan Stage, Ashgill Series, Ladyburn, Girvan district. Ventral stereo-pair, x 5.

8, 9, 11. Lectotype, incomplete, partially exfoliated cranidium, BM In23370, Gray Colln., Upper Drummuck Group, Rawtheyan Stage, Ashgill Series, Drummuck, Girvan district. Left lateral, dorsal views, x 2; enlargement of central glabellar area, x 6. Note fine, closely-spaced tubercular ornament. Figured Nicholson & Etheridge 1879, pl. 10, figs. 4, 4a as Calymene blumenbachii, and syntype of Calymene blumenbachii, auct., var. nov. drummuckensis Reed, 1906, pl. 18, fig. 3.

10. Free cheek, WM unnumbered, same horizon and locality as for fig. 1. 'Dorsal' stereo-pair, x 2.

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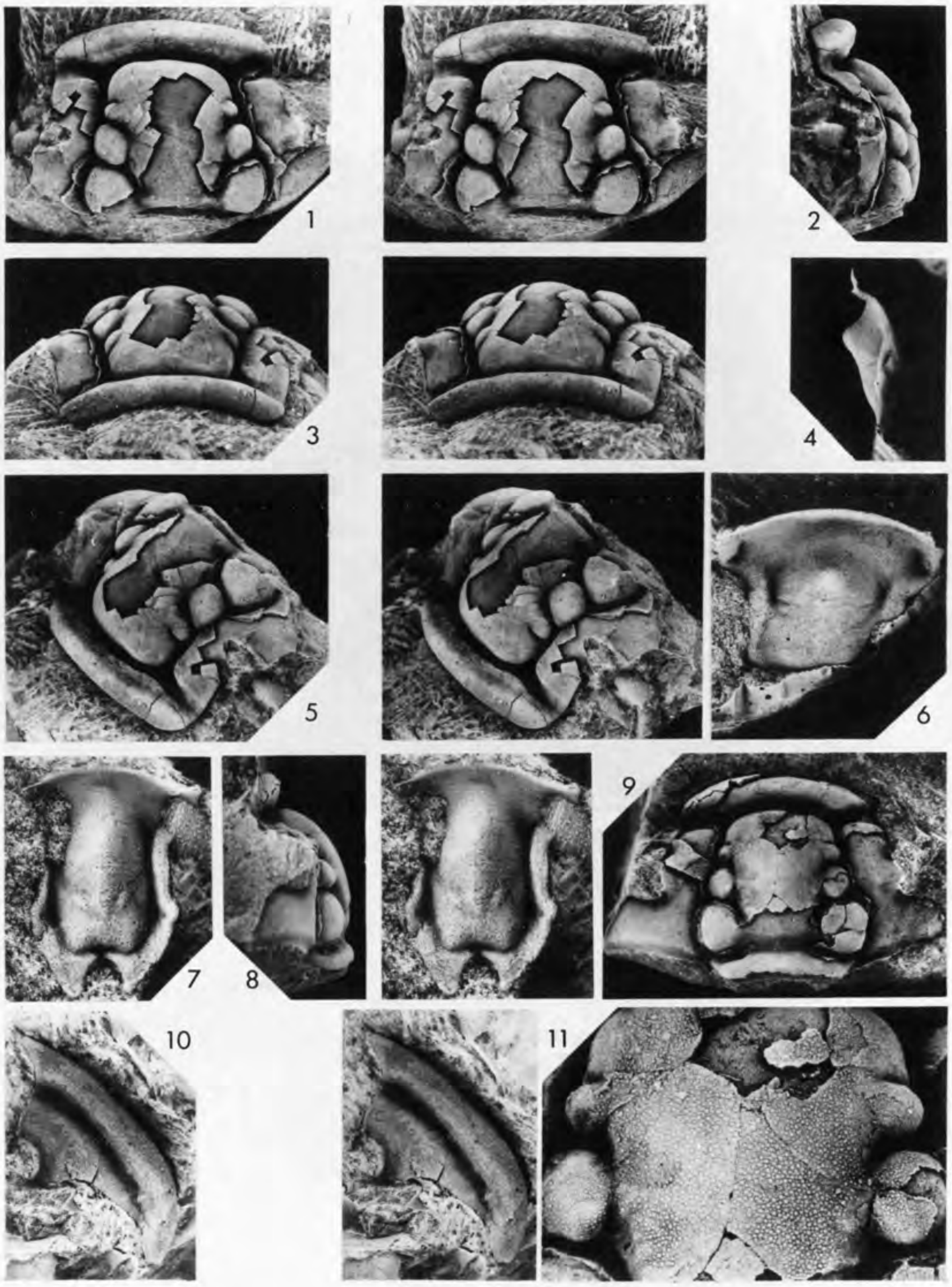

PLATE 5

Figs. 1-12. <u>Diacalymene</u> <u>drummuckensis</u> (Reed, 1906)

1-3, 9. Cephalon and five thoracic segments, internal mould, RSM 1899.91. 11A, Upper Drummuck Group, Ladyburn, Girvan district. Dorsal stereo-pair of cephalon, right lateral view, ventral view of rostral plate, right oblique view of cephalon, x $1\frac{1}{2}$.

4-7. Incomplete cranidium, RSM 1968, 50, 34A, same horizon and locality as for fig. 1. Frontal, right lateral views, dorsal stereo-pair, right oblique view, x 2.

8, 11, 12. Paralectotype, pygidium, BM In23383, Gray Colln., Starfish Bed, Upper Drummuck Group, Rawtheyan Stage, Ashgill Series, Thraive, Glen, Girvan district. Dorsal view, posterior stereo-pair, right lateral view, x $1\frac{1}{4}$. Syntype of <u>C</u>. <u>drummuckensis</u> Reed, 1906. Figured Reed 1906, pl. 18, fig. 4.

10. Distorted cephalon and four thoracic segments, 'Silcoset' rubber cast of external mould, BM In43025, Gray Colln., same horizon and locality as for fig. 8. Dorsal view, x 2.

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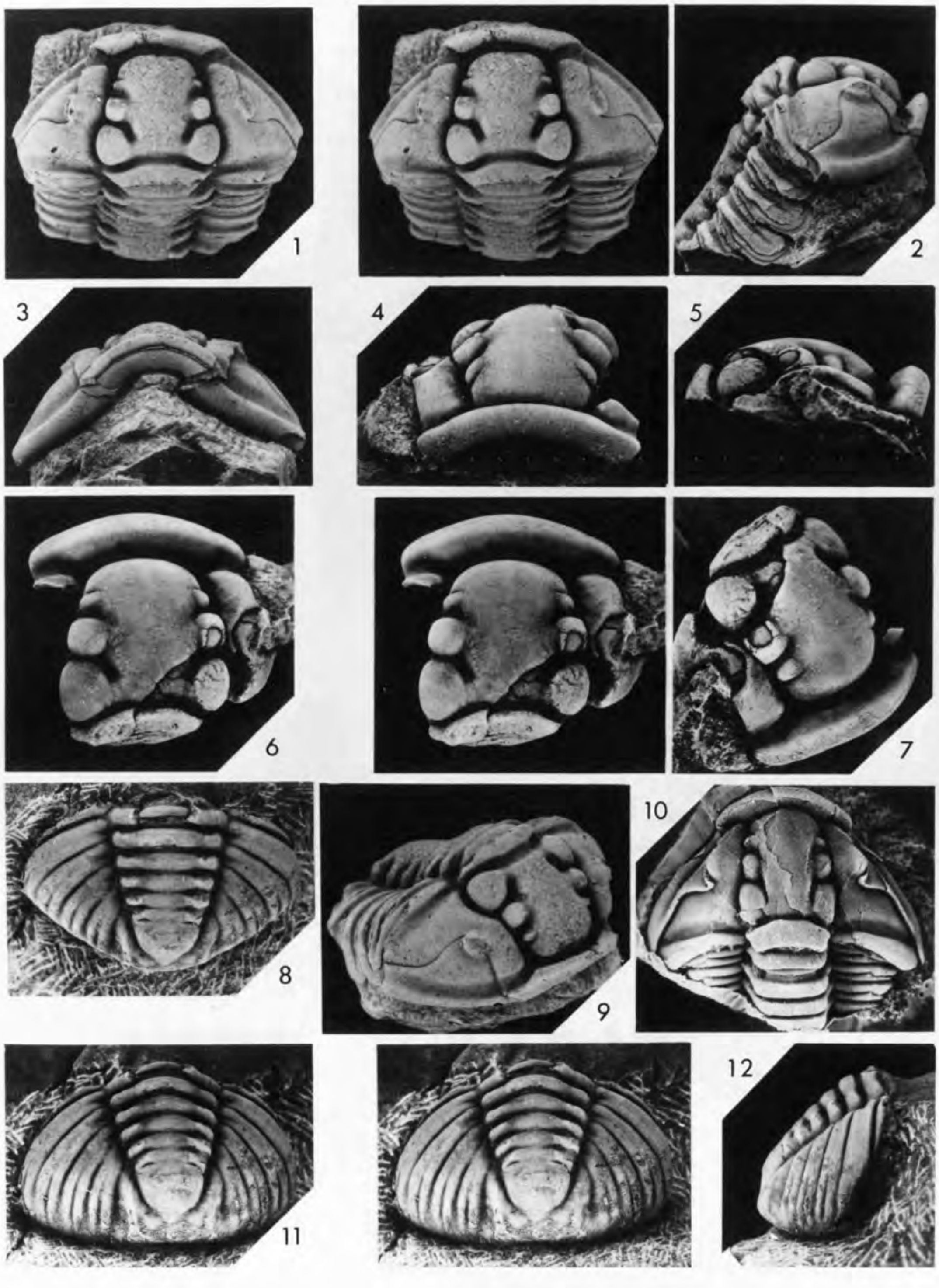

PLATE 6

Figs. 1-3, 5, 6. Diacalymene consimilis (Cooper, 1930)

1, 2, 5, 6. Incomplete cranidium, BM It7392, White Head Formation, Upper Ordovician, Mont Joli, Perce, Quebec. Right oblique stereo-pair, right lateral, frontal, dorsal views, x 2.

3. Incomplete cranidium, BM It7393, same horizon and locality as for fig. 1. Dorsal stereo-pair, x 2.

Figs. 4, 7-9. Diacalymene drummuckensis (Reed, 1906)

4, 9. Almost complete specimen, internal mould, HM A5081, Starfish Bed, Upper Drummuck Group, Ladyburn, Girvan district. Dorsal view of thorax, left lateral view, x 1½.

7, 8. Paralectotype, rostral plate, hypostome, and ventral part of left free cheek, 'Silcoset' rubber cast of external mould, BM In23381, Gray Colln., Starfish Bed, Upper Drummuck Group, Rawtheyan Stage, Ashgill Series, Thraive Glen, Girvan district. Postero-ventral view, ventral stereo-pair, x 4. Syntype of C. drummuckensis Reed, 1906. Internal mould counterpart of this specimen was figured by Reed 1906, pl. 17, fig. 14.

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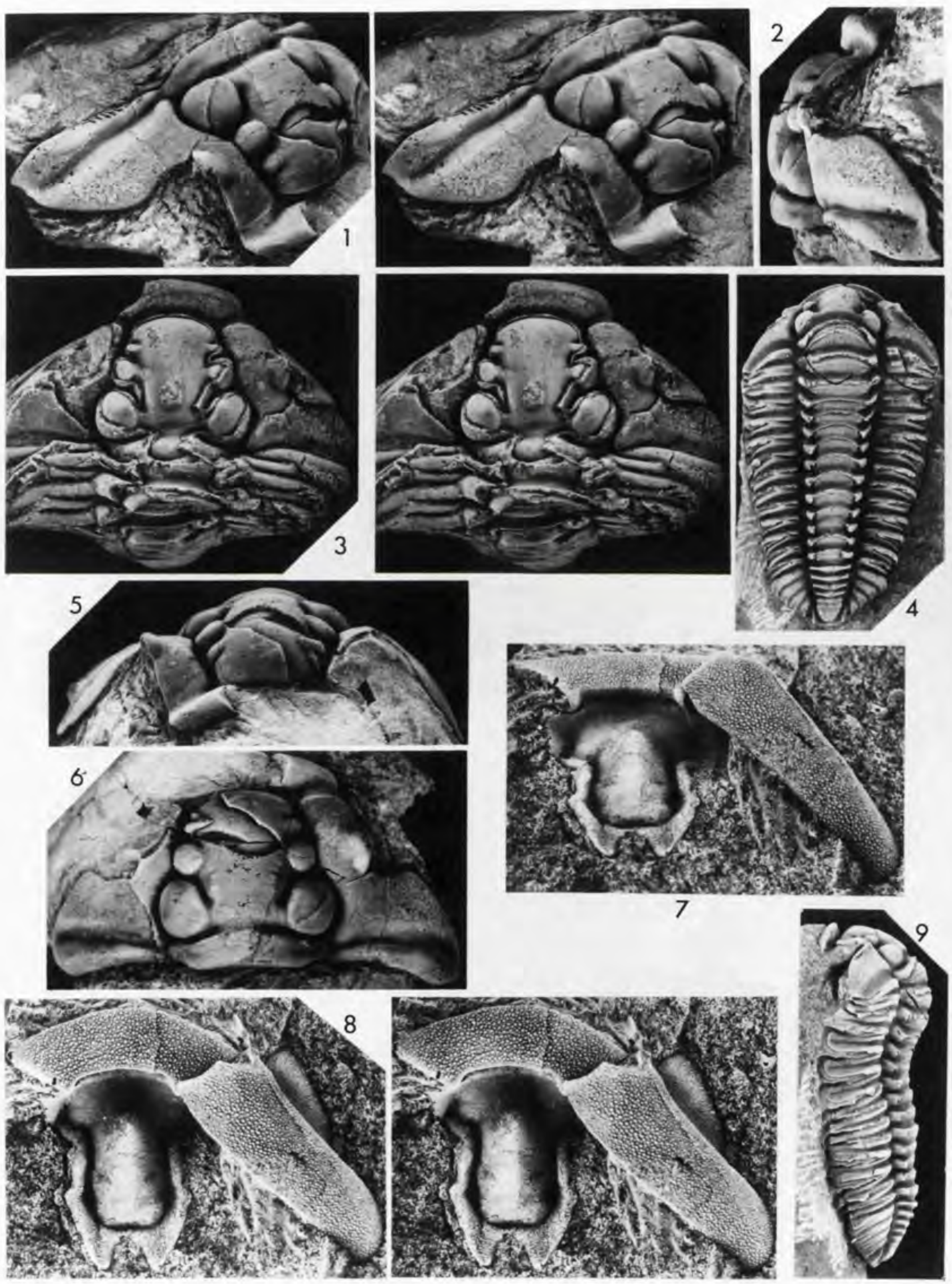

PLATE 7

Figs. 1, 4, 8. Diacalymene aff. D. drummuckensis (Reed, 1906)

1. Incomplete cranidium, internal mould, RM Ar14993, Dalmanitina Beds (Ashgillian), Alleberg, Vastergotland, Sweden. Dorsal stereo-pair, x 2.

4. Incomplete cranidium, internal mould, RM Ar15224, same horizon and locality as for fig. 1. Dorsal view, x 2.

8. Incomplete cranidium, internal mould, RM Ar15112, same horizon and locality as for fig. 1. Dorsal view, x 3.

Figs. 2, 3, 5-7, 9, 10. Diacalymene asperula (Vanek, 1965)

2, 3, 10. Incomplete cranidium, internal mould, L Mk 1, uppermost layers of the Kraluv Dvur Formation (= Rawtheyan in age), Kosov, near Kraluv Dvur, Czechoslovakia. Coll. L. Marek. Left lateral, dorsal, left oblique views, x 1½.

5, 6. Incomplete cranidium, 'Silcoset' rubber cast of external mould (fig. 5) and internal mould (fig. 6), L Mk 3, same horizon, locality and collector as for fig. 2. Dorsal view, x 1½.

7, 9. Incomplete cranidium, internal mould, L Mk 2, same horizon, locality and collector as for fig. 2. Frontal, dorsal views, x 1½.

7

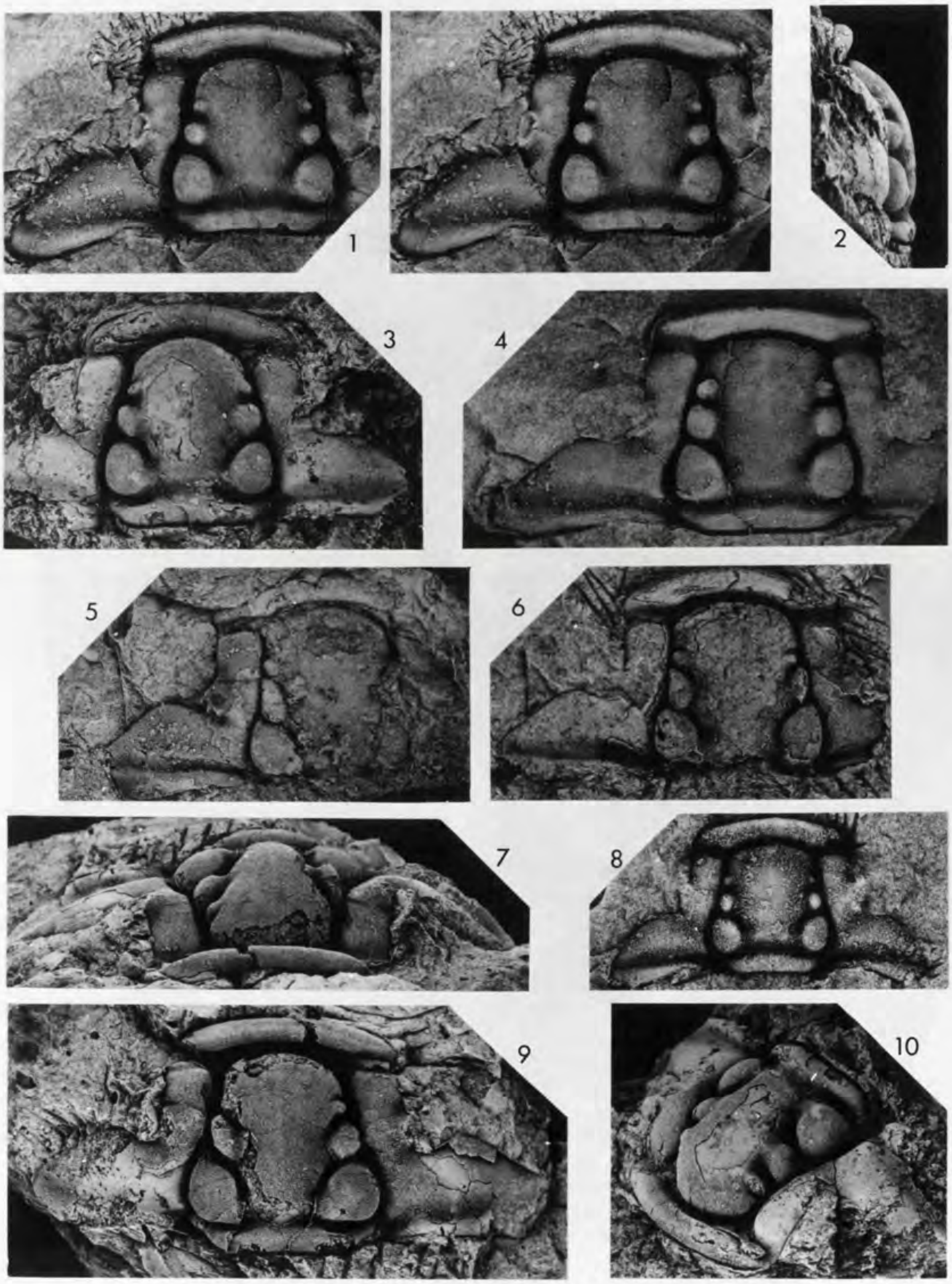

PLATE 8

Figs. 1-4, 6-8. Diacalymene aff. D. drummuckensis (Reed, 1906)

1-4, 6. Incomplete cephalon, RM Ar18581, Dalmanitina Beds (Ashgillian), Borenshult, Östergotland, Sweden. Right oblique, dorsal, frontal stereo-pairs (cephalon), ventral stereo-pair (rostral plate), x $1\frac{1}{4}$; left lateral view, x 2.

7, 8. Incomplete pygidium, RM Ar18571, same horizon and locality as for fig 1. Posterior stereo-pair, dorsal view, x 2.

Fig. 5. Diacalymene sp. A

Rostral plate and outer side of anterior border of incomplete cephalon, RM Ar1778, Mulde Beds, Djupvik, Eksta, Gotland. Ventral stereo-pair, x 2.7. See also Pl. 9, figs. 3, 7-9.

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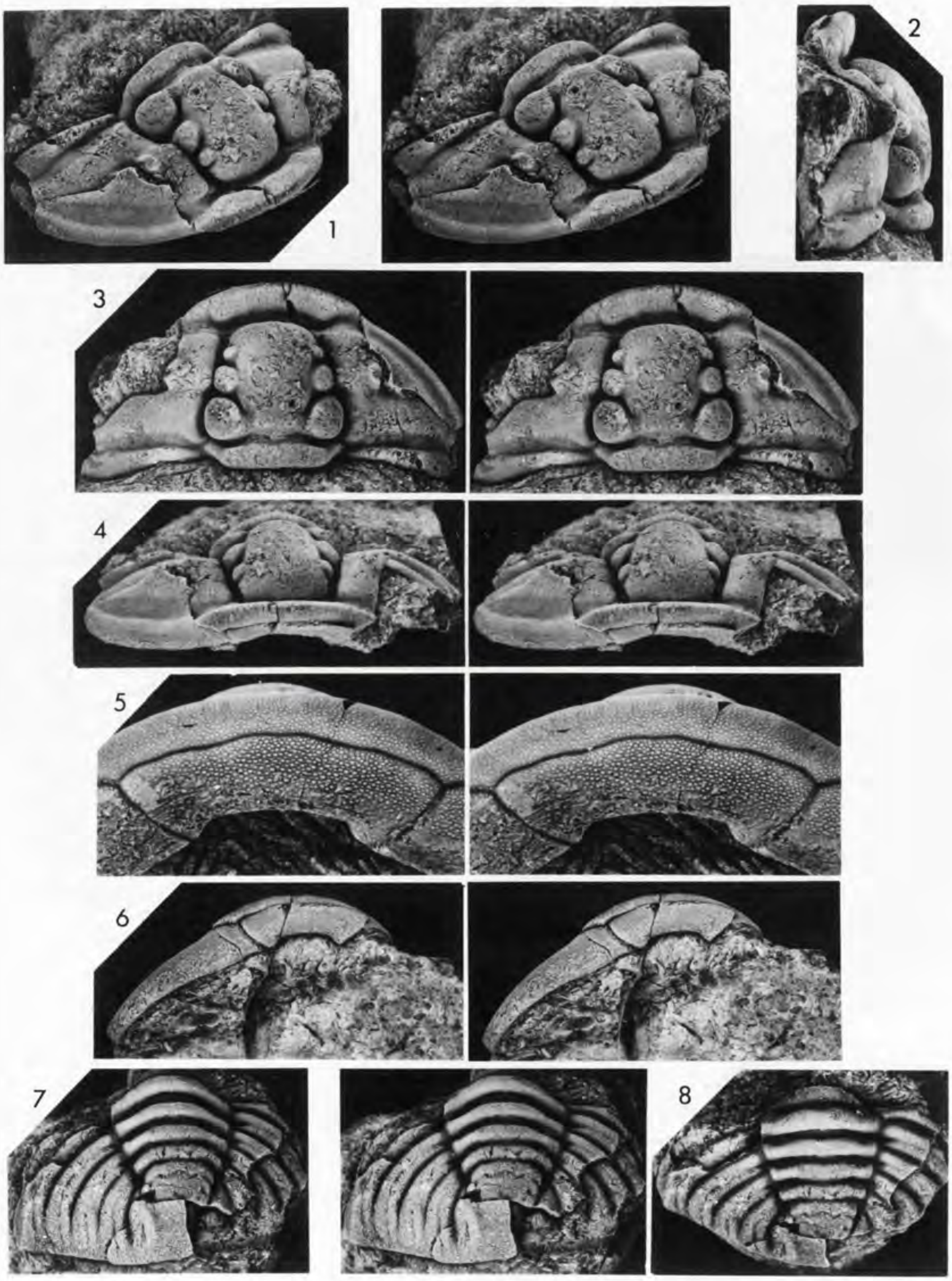

PLATE 9

Figs. 1, 2, 4-6. Diacalymene allportiana (Salter, 1865)

Holotype, complete specimen, BM 58984, Wenlock Limestone, Dudley. Dorsal stereo-pair, right lateral, frontal, right oblique, posterior views, x 1½. Figured Salter 1865, p. 95. text-fig. unnumbered; Shirley 1933, pl. 1, figs. 12-14 as Calymene allportiana.

Figs. 3, 7-9. Diacalymene sp. A

Incomplete cephalon, partially exfoliated, IPU Ar1778, Mulde Beds, Djupvik, Eksta, Gotland. Frontal view, dorsal view, left oblique stereo-pair, left lateral view, x 1¼. See also Pl. 8, fig. 5.

9

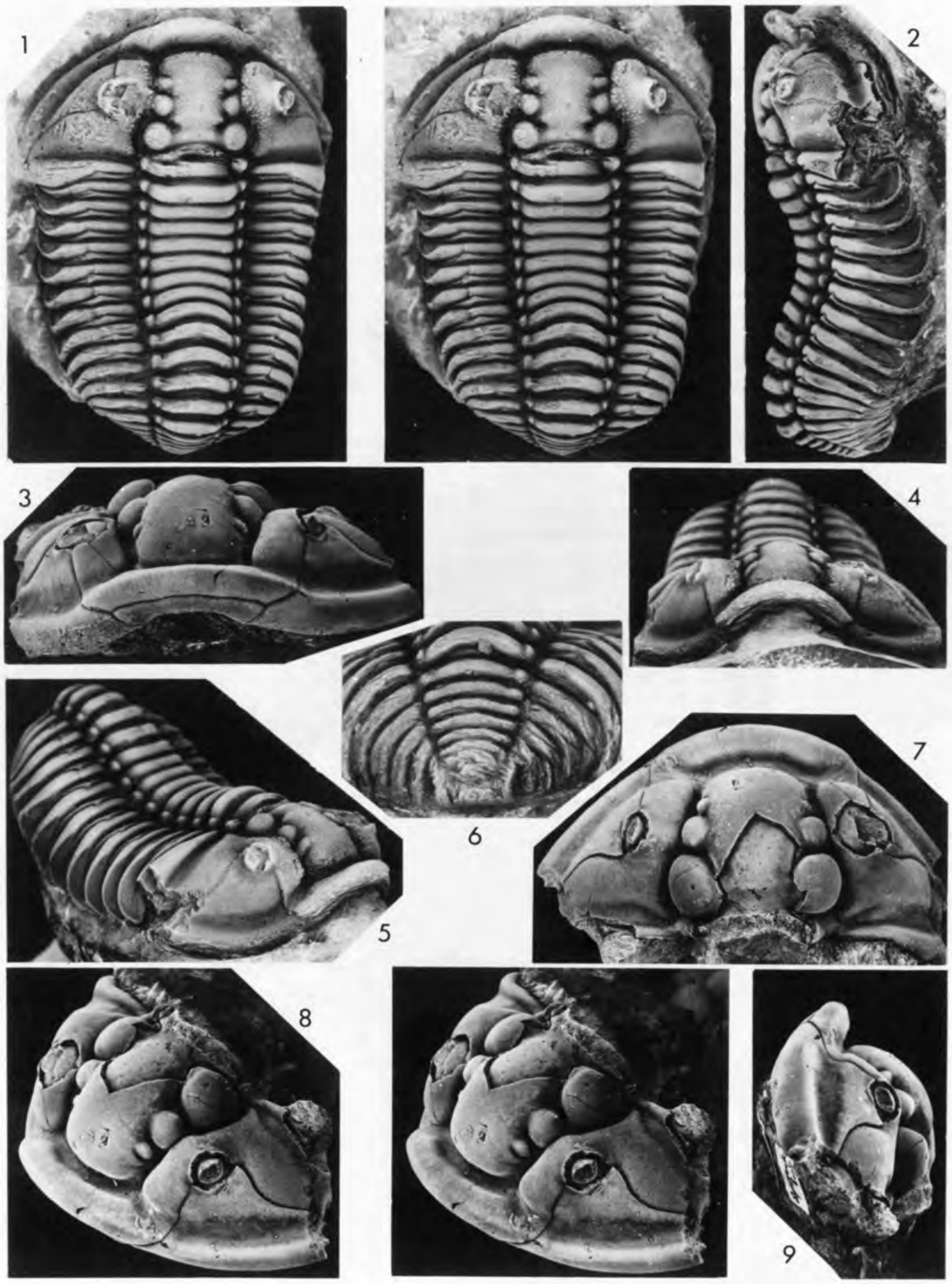

PLATE 10

Figs. 1-9. Diacalymene diademata (Beyrich, 1846)

1-4. Incomplete cranidium, partially exfoliated, NMW 71. 8G. 376, high in the Liten Formation, upper Wenlock (radians-testis zone), above path leading from Svaty Jan pod Skalou to Vraz, SW of Prague, Czechoslovakia. Coll. R.M. Owens. Dorsal, frontal, right oblique stereo-pairs, x 1¼; left lateral view, x 1½.

5, 7. Incomplete hypostome, partially exfoliated, NMW 71. 8G. 242, Liten Formation, Wenlock Series (radians-testis zone), old quarry by roadside, about half a mile N of Svaty Jan pod Skalou, SW of Prague, Czechoslovakia. Coll. R.M. Owens. Ventral view, x 4½; lateral view, x 5.

6. Paralectotype, incomplete cranidium, cuticle remaining in axial and preglabellar furrows, MB 498. 2. B.K. p. 79, Liten Formation, Wenlock Series, Svaty Jan, SW of Prague, Czechoslovakia. Dorsal view, x 1¼. Original syntype of Calymene diademata Beyrich, 1846.

8. Free cheek, plaster cast, partially exfoliated, NMP It337, high in the Liten Formation, upper Wenlock, Svaty Jan pod Skalou, SW of Prague, Czechoslovakia. 'Dorsal' stereo-pair, x 1½. Figured Barrande 1852, pl. 19, fig. 17 as Calymene diademata.

9. Incomplete pygidium, plaster cast, NMP 35050 (Barrande Colln), Liten Formation, Wenlock Series, Bubovice, Czechoslovakia. Left oblique view, x 2.

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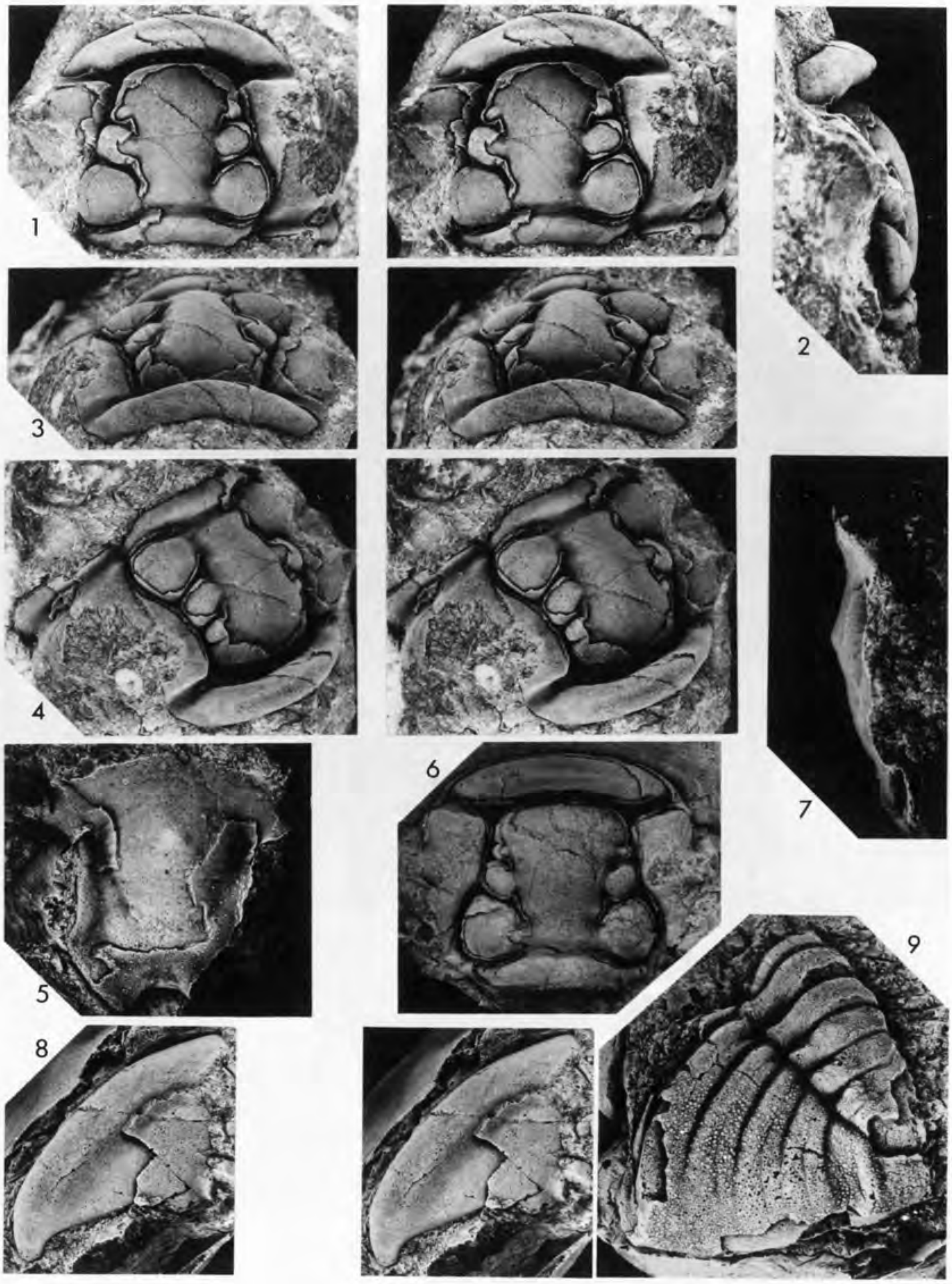

PLATE 11

Figs. 1-10. *Diacalymene diademata* (Beyrich, 1846)

1, 4, 9. Incomplete, partially exfoliated cranidium, NMW 71. 8G. 377, high in the Liten Formation, upper Wenlock (*radians-testis* zone), above path leading from Svaty Jan pod Skalou to Vraz, SW of Prague, Czechoslovakia. Coll. R.M. Owens. Dorsal stereo-pair, frontal view, x $1\frac{1}{2}$; right oblique view, x $2\frac{1}{2}$.

2, 6, 10. Lectotype, incomplete cranidium, internal mould, MB 498. 1. B.K. p. 79. K. 187., Liten Formation, Wenlock Series, Svaty Jan, Czechoslovakia. Left lateral view, x 2; frontal, dorsal views, x $1\frac{1}{2}$. Figured Beyrich 1846, pl. 2, figs. 4a, c.

3. Hypostome, NMP 35050 (Barrande Colln.), Liten Formation, Wenlock Series, Svaty Jan, Czechoslovakia. Ventral stereo-pair, x $3\frac{1}{2}$.

5, 7, 8. Paralectotype, pygidium, internal mould, MB. 499. 1. B.K. p. 79. K. 188., same horizon and locality as for fig. 2. Posterior stereo-pair, dorsal view, x $1\frac{1}{4}$; right lateral view, x 2. Figured Beyrich 1846, pl. 2, fig. 4b.

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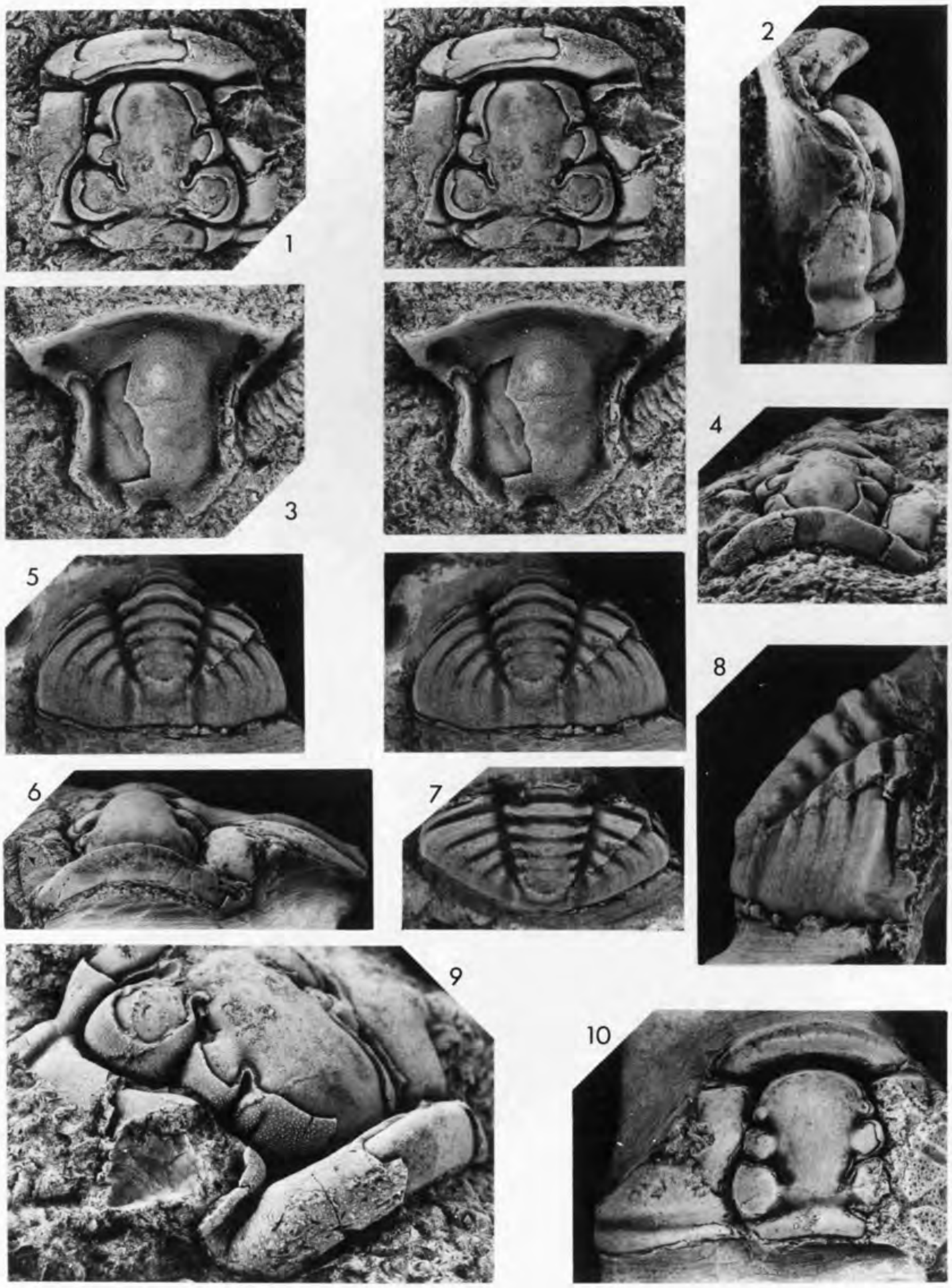

PLATE 12

Figs. 1-10. Diacalymene crassa Shirley, 1936

1-3, Holotype, incomplete cranidium, internal mould, GSM
5. 54910 (formerly GSM Pg2364), Gasworks Mudstone, upper Rhuddanian Stage, Llandovery Series, by the side of Frolic path, 383-390 yards from Higgons Well, half a mile SE of Haverfordwest, S Wales. Dorsal stereo-pair, left lateral view, frontal stereo-pair, left oblique view, x $2\frac{3}{4}$. Figured Shirley 1936, pl. 29, figs. 21, 22.

4, 10. Incomplete, distorted cranidium, 'Silcoset' rubber cast of external mould, GSM TCC 1941, Rhuddanian Stage (?), Llandovery Series, Black Becks gate, $2\frac{1}{2}$ miles E by S of Haverfordwest, S Wales. Dorsal, right oblique views, x 2.

6, 8. Cephalon, internal mould, SM A32717 (Turnbull Colln. 169), Llandovery Series, loch D, excavation for second boathouse, the Frolic, Haverfordwest, S Wales. Ventral view, x $2\frac{1}{4}$; dorsal view, x $1\frac{3}{4}$.

7. Incomplete cephalon, 'Silcoset' rubber cast of external mould, BM It8647, Gasworks Mudstone, Rhuddanian Stage, Llandovery Series, opposite the Gasworks gate, Haverfordwest, S Wales. Dorsal view, x 2. Mentioned Temple 1970, p. 65.

9. Incomplete cranidium, internal mould, SM A54095, Gasworks Mudstone, Rhuddanian Stage, Llandovery Series, lane section, near the Gasworks, Haverfordwest, S Wales. Coll. D.L. Jones, 1963. Dorsal stereo-pair, x $2\frac{1}{4}$.

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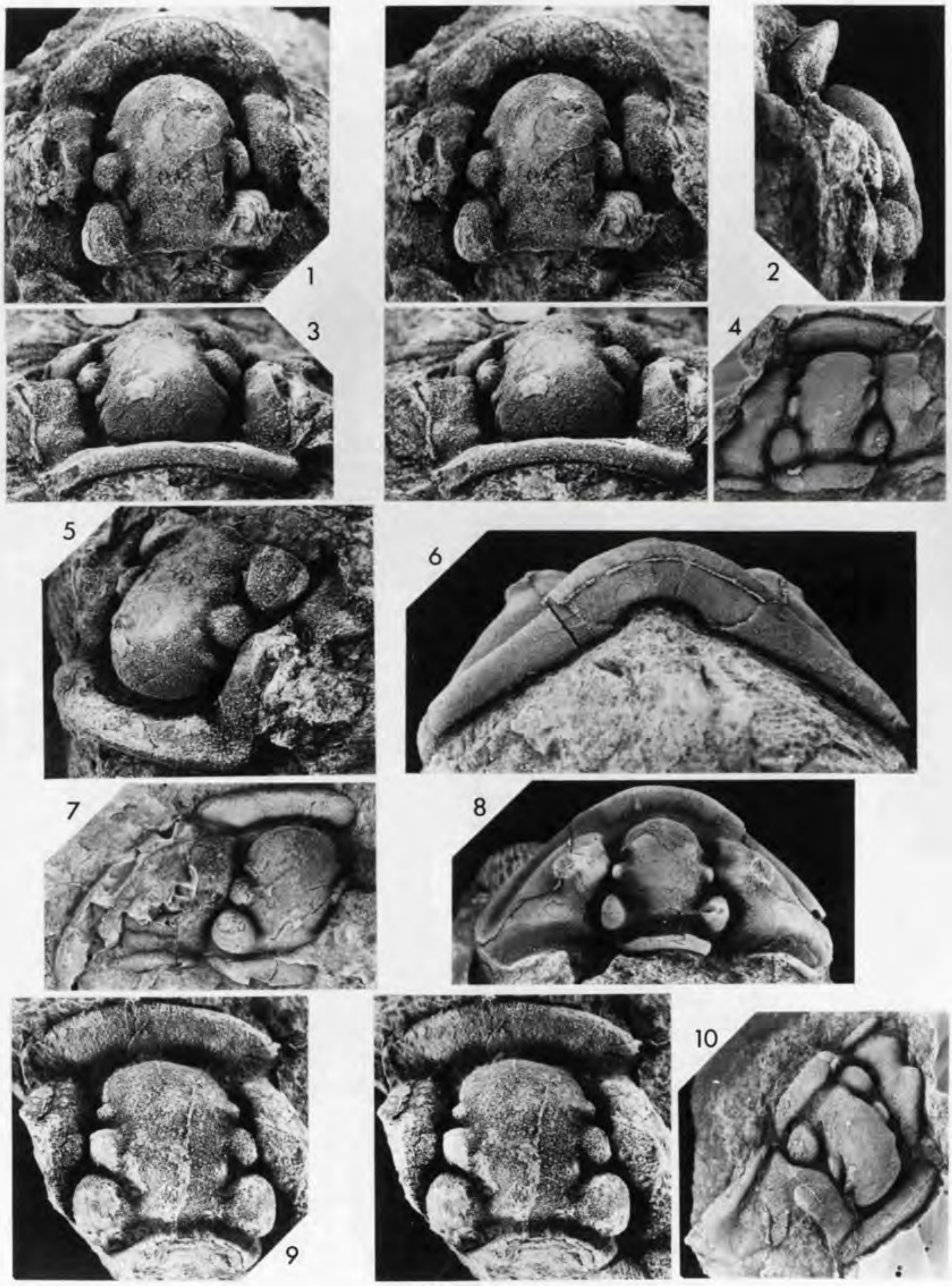

PLATE 13 (continued)

Figs. 6, 7, 10-12. Diacalymene gibberosa sp. nov.

6. Incomplete cranidium, cuticle remaining on left fixed cheek and axial furrow, PMO 41626 Stage 6 (lower Llandovery), uppermost layer of the eastern Headland, S side of Sjursøya, N end of Bunne fiord, Oslo district, Norway. Coll. J. Kiaer, 1905. Dorsal view, x 2½.

7. Pygidium, PMO 20945, Stage 6a/β (lower Llandovery), uppermost layer, eastern headland, S side of Sjursøya, N end of Bunne fiord, Oslo district, Norway. Coll. J. Kiaer, 1905. Posterior view, x 3.

10-12. Small cranidium, PMO 20945, on same block as fig. 7. Frontal, dorsal views, x 4 ; left oblique view, x 10. Tubercles coarser than on more mature specimens.

PLATE 13

Figs. 1, 3, 8. Diacalymene cf. D. crassa Shirley, 1936

1. Incomplete cranidium, internal mould, PMO 65535, Stage 6b (lower Llandovery), Gullerasen, Oslo district, Norway. Coll. N. Spjeldnaes, 1945. Dorsal view, x 3.

3, 8. Incomplete cranidium, internal mould, PMO 91112, Stage 6 (lower Llandovery), Vakas ved Jernbanelinjen, Asker district, Oslo Region, Norway. Dorsal, left oblique views, x 4.

Figs. 2, 4, 5, 9, 13. Diacalymene crassa Shirley, 1936

2, 4. Incomplete cranidium, internal mould, GSM 54911 (formerly TCC 1776), Gasworks Mudstone, Rhuddanian Stage, Llandovery Series, from Brook 400 yards E by S of Cotts Park, 1½ miles E of Haverfordwest, S Wales. Dorsal, left lateral views, x 3. Figured Shirley 1936, pl. 29, fig. 23.

5, 9, 13. Complete specimen, internal mould, BM In58236a, Gasworks Mudstone, about 10 feet below base of Gasworks Sandstone, Rhuddanian Stage, Llandovery Series, opposite gate of Gasworks, Haverfordwest, S Wales. Dorsal, right oblique, right lateral views, x 1½.

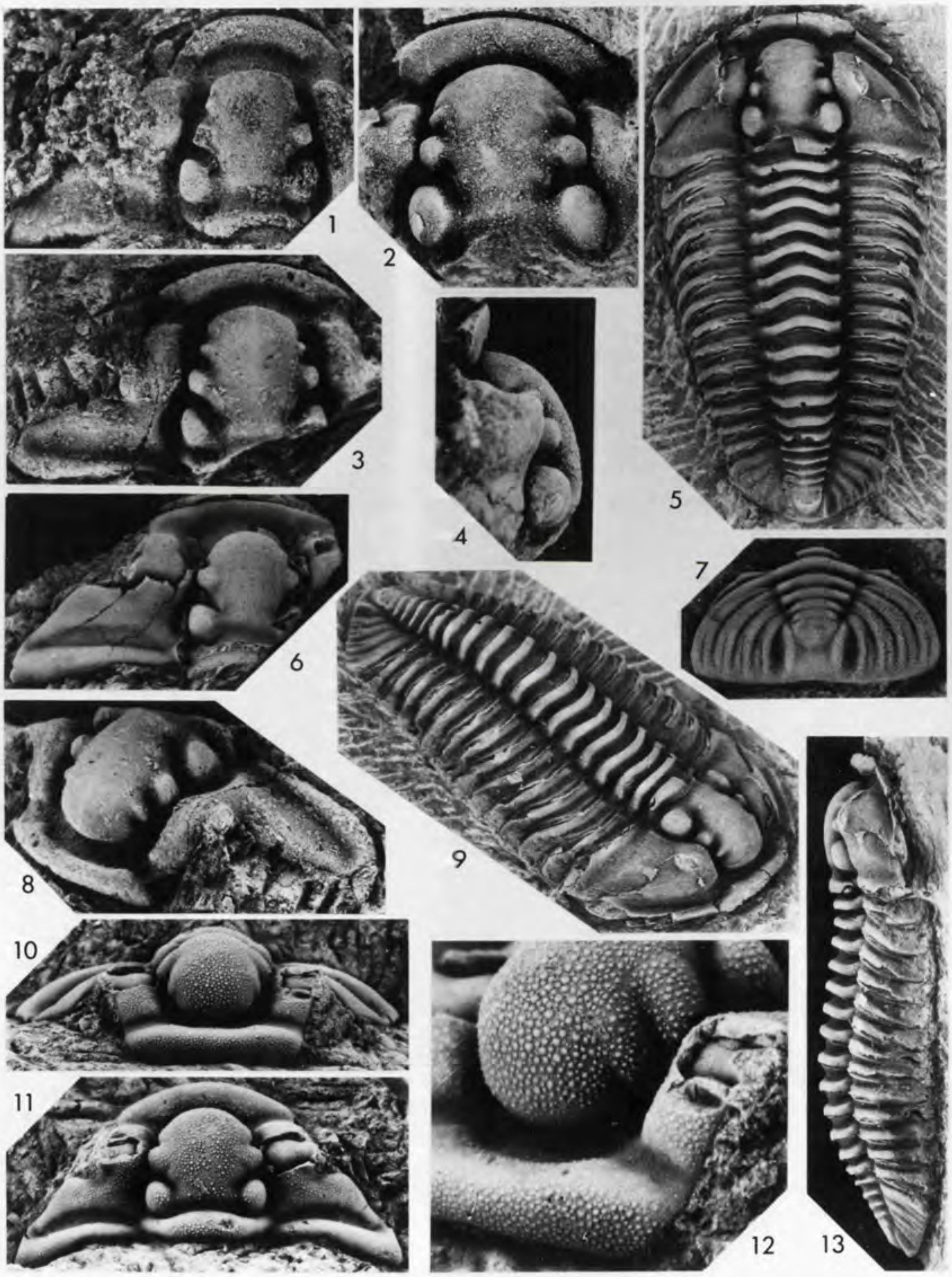
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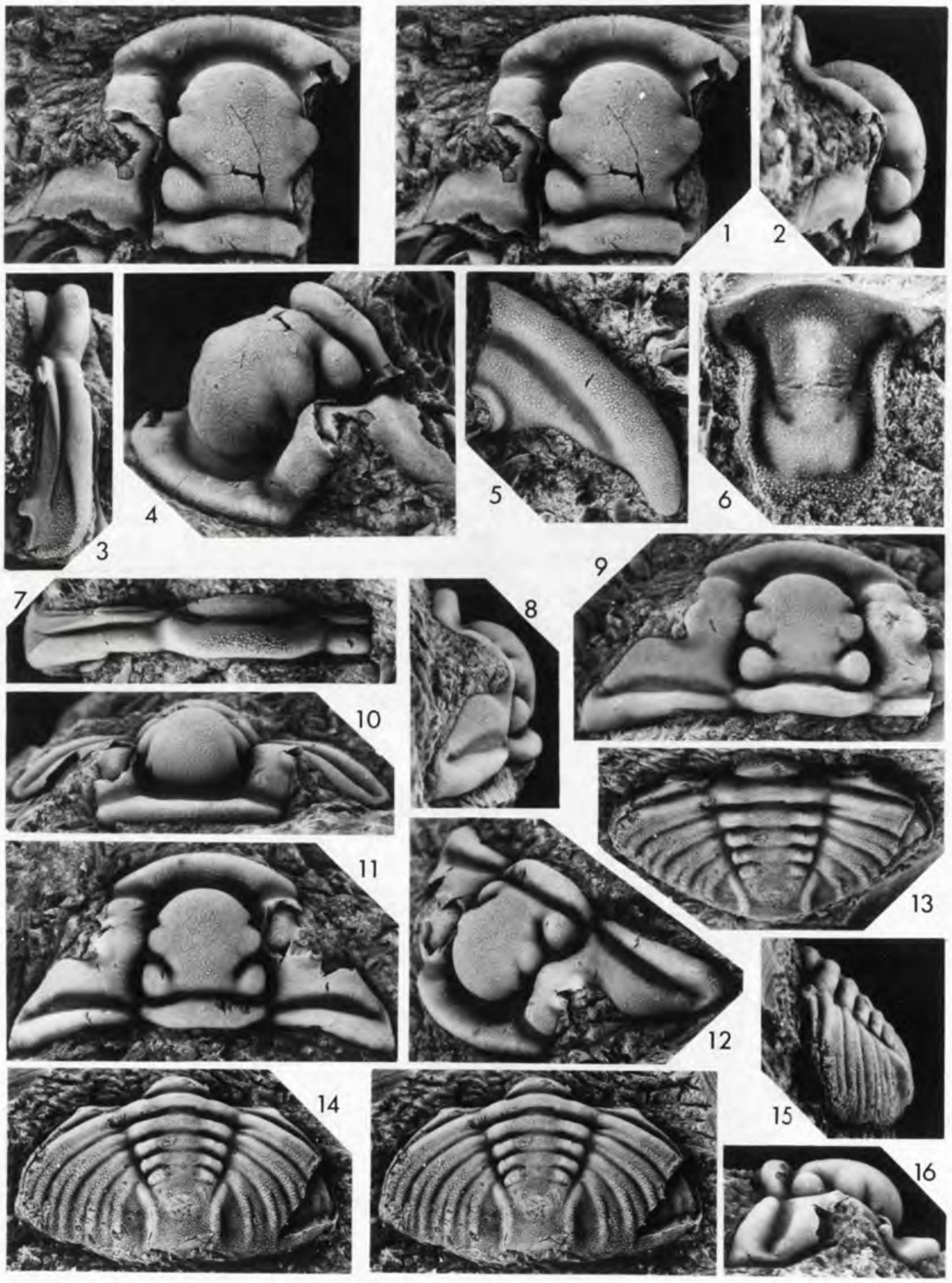
PLATE 14

Figs. 1-16. Diacalymene gibberosa sp. nov.

1, 2, 4.	Holotype, incomplete cranidium, PMO 41620, Stage 6a/β (lower Llandovery), uppermost layer of eastern headland, S side of Sjursøya, N end of Bunne fiord, Oslo district, Norway. Coll. J. Kiaer, 1905. Dorsal stereo-pair, left lateral, left oblique views, x 3½.
3, 7.	Thoracic segment, PMO 91113, same horizon, locality and collector as for fig. 1. Left lateral, dorsal views, x 4.
5.	Free cheek, PMO 20947, same horizon, locality and collector as for fig. 1. 'Dorsal' view, x 5.
6.	Hypostome, PMO 41634, same horizon locality and collector as for fig. 1. Ventral view, x 10.
8, 9.	Incomplete cranidium, PMO 20948, same horizon, locality and collector as for fig. 1. Left lateral, dorsal views, x 3.
10-12, 16.	Almost complete cranidium, PMO 41624, same horizon, locality and collector as for fig. 1. Frontal, dorsal, left oblique right lateral views, x 3½.
13-15.	Pygidium, PMO I0838, same horizon, locality and collector as for fig. 1. Dorsal view, posterior stereo-pair, left lateral view, x 3.

14



CHAPTER E PLATES 1-43

THE GENUS *CALYMENE* FROM THE SILURIAN AND LOWER DEVONIAN OF BRITAIN, SWEDEN AND CZECHOSLOVAKIA.

PLATE 1

Figs. 1-14. Calymene subdiademata subdiademata McCoy, 1851

1, 2. Complete specimen, internal mould, HM A5462a, Newlands Formation, Idwian Stage, Llandovery Series, 'Dailly', near Girvan. Dorsal stereo-pair, right lateral view, x 2½.

3, 4, 7. Pygidium, internal mould, BU Begg Colln. No. 5, Newlands Formation, Idwian Stage, Llandovery Series, Newlands, N of New Dailly, Girvan district. Posterior, dorsal, left lateral views, x 3¼.

5, 6. Hypostome, 'Silcoset' rubber cast of external mould, BM It9091 (Gray Colln.), same horizon and locality as for fig. 3. Ventral stereo-pair, lateral view, x 5.

8, 12-14. Incomplete cranidium, 'Silcoset' rubber cast of external mould (fig.8) and partly exfoliated counterpart (figs. 12-14), HM A12002 a-b, same horizon and locality as for fig. 1. Dorsal stereo-pair, x 2½; dorsal, left oblique, anterodorsal views, x 2.

9. Lectotype, cranidium, internal mould, SM A34872, probably Newlands Formation, Idwian Stage, Llandovery Series, "Mulloch, Dalquharran" Girvan district. Dorsal view, x 2½. Described McCoy 1851, p. 166 as C. subdiademata (McCoy). Listed Salter 1873, p. 77 as C. blumenbachii Brongn.

10. Cranidium, 'Silcoset' rubber cast of external mould, BM In43652 (Gray Colln.), same horizon and locality as for fig. 3. Dorsal stereo-pair, x 2½.

11 Cranidium, internal mould, BM In23337 (Gray Colln.), same horizon and locality as for fig. 3. Dorsal view, x 2½. Figured Reed 1906, pl. 17, fig. 13 as C. blumenbachii.

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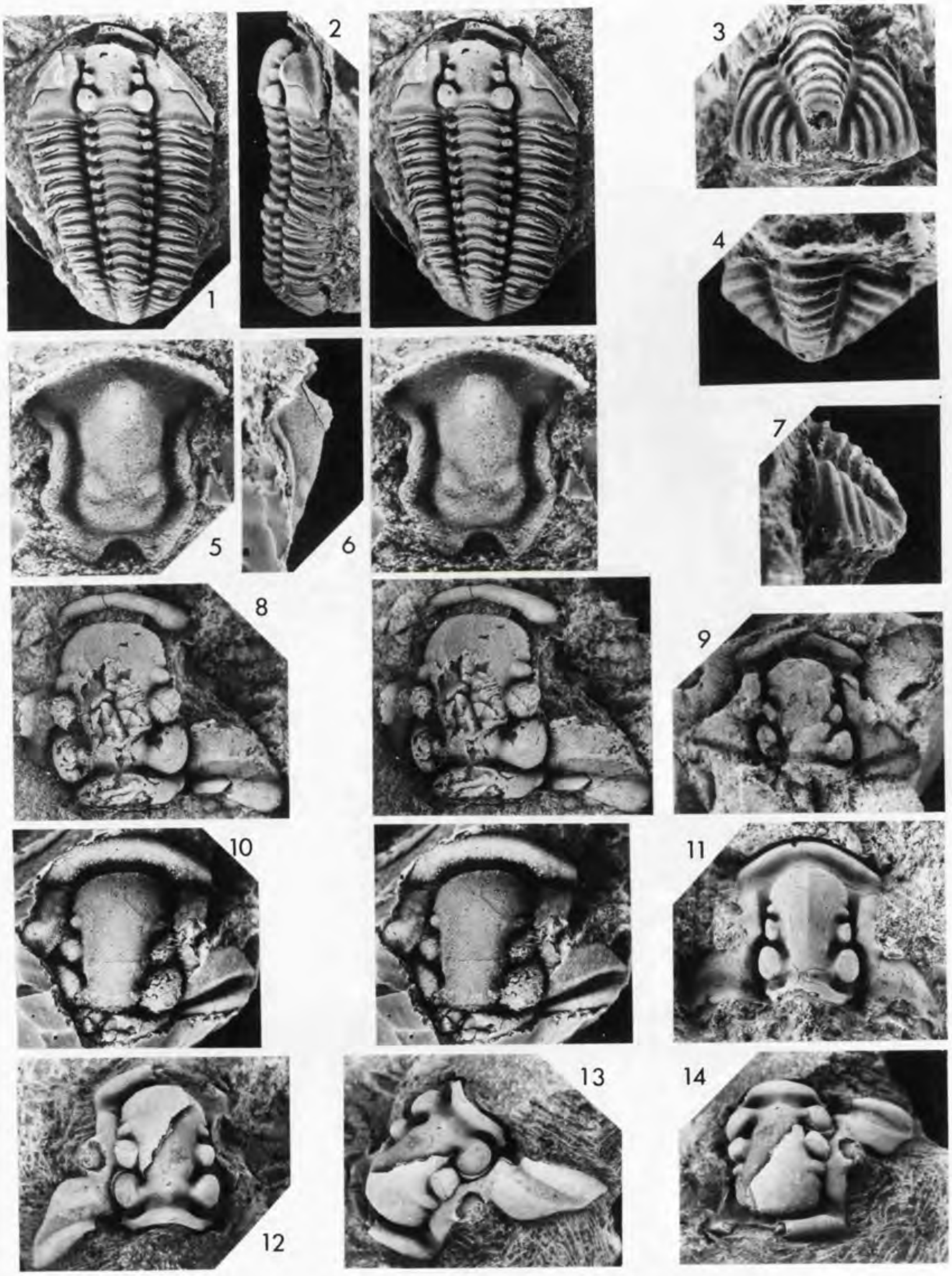

PLATE 2

Figs. 1-6, 8, 10, 11. Calymene subdiademata McCoy replicata Shirley

1-3, 6. Holotype, internal mould of incomplete cephalon and three attached thoracic segments, SM A14922a, Fronian Stage (near base of), Llandovery Series, at the sharp bend in the stream, 360 yards - above the footbridge S of Lletty'-r-hyddod, near Llandovery, Carmarthenshire. Dorsal stereo-pair, left oblique view, frontal stereo-pair, right lateral view, x 2. Figured Shirley 1936, pl. 30, figs. 3 (internal mould), 2 and 5 (cast of external mould - SM A14992b - which is now missing).

4. Cranidium, internal mould, P La 4/23, same horizon and locality as for fig. 1. Dorsal view, x 3½.

5, 11. Complete, distorted specimen, 'Silcoset' rubber cast of external mould, P La 4/3, same horizon and locality as for fig. 1. Dorsal stereo-pair, dorsolateral view, x 1½.

8, 10. Incomplete cephalon and nine thoracic segments, 'Silcoset' rubber cast of external mould, P La 4/38, same horizon and locality as for fig. 1. Dorsal, left oblique stereo-pairs, x 2.

Figs. 7, 9. Calymene subdiademata subdiademata McCoy, 1851

Cranidium, internal mould with cuticle remaining on right part of preglabellar area, BM In43631, Newlands Formation, Idwian Stage, Llandovery Series, Newlands, N of New Dailly, Girvan district. Dorsal, right lateral views, x 2.

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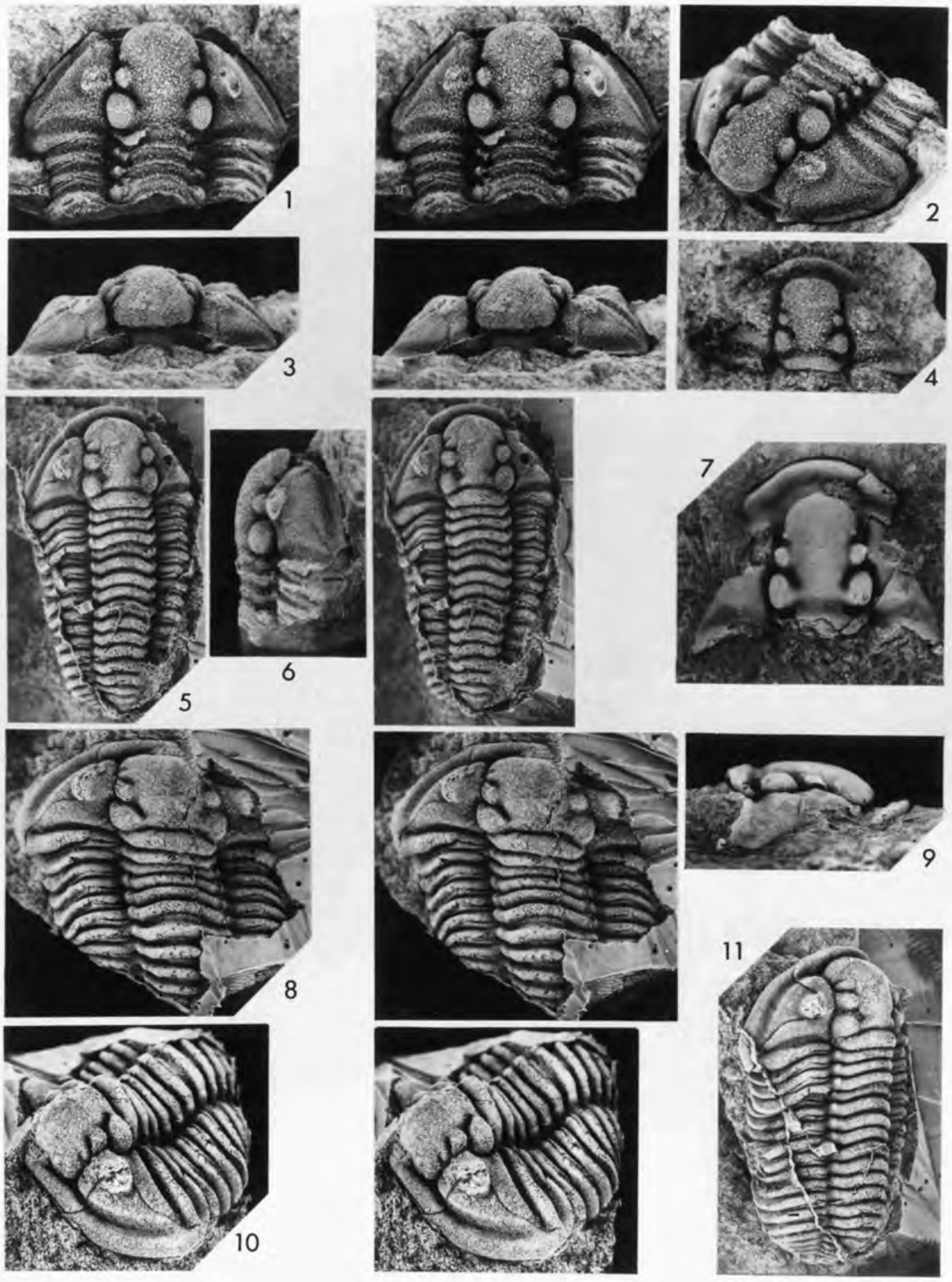

PLATE 3

Figs. 1-9. Calymene frontosa Lindström, 1885

1, 2 Lectotype, complete enrolled specimen, RM Ar6210,
4. (? Lower) Visby Beds, Visby, Gotland. Dorsal stereo-pair, left lateral, frontal views, x 2½. Figured Lindström 1885, pl. 15, figs. 1-3.

3. Hypostome, RM Ar27054, probably Visby Beds, locality unknown, Gotland. Ventral stereo-pair, x 6.

5-9. Complete enrolled specimen, RM Ar47000, Visby Beds, Norderstrand, Visby, Gotland. Ventral, left lateral, left oblique, dorsal, frontal views x 2½.

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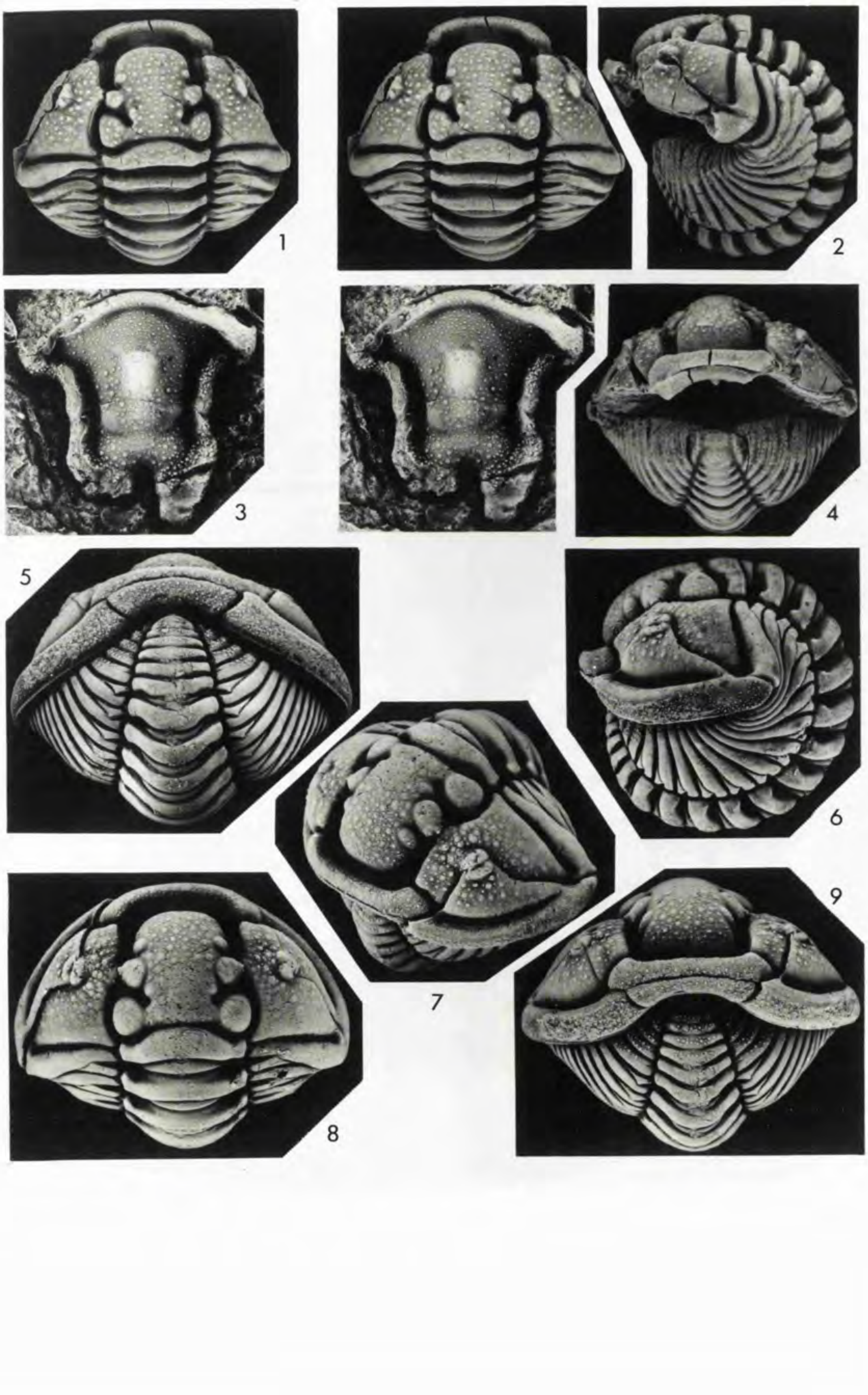

PLATE 4

Figs. 1-9. Calymene frontosa Lindström, 1885

1, 3 6, 9.	Complete enrolled specimen, RM Ar27038, Visby Beds, Visby, Gotland. Dorsal, frontal, right oblique stereo-pairs, left lateral view, x $2\frac{1}{2}$. Original of Lindström.
2, 4, 5, 7, 8.	Complete enrolled specimen, RM Ar47003, Visby Beds, Norderstrand, Visby, Gotland. Left lateral, ventral-oblique, ventral, dorsal, frontal views, x $2\frac{1}{2}$.

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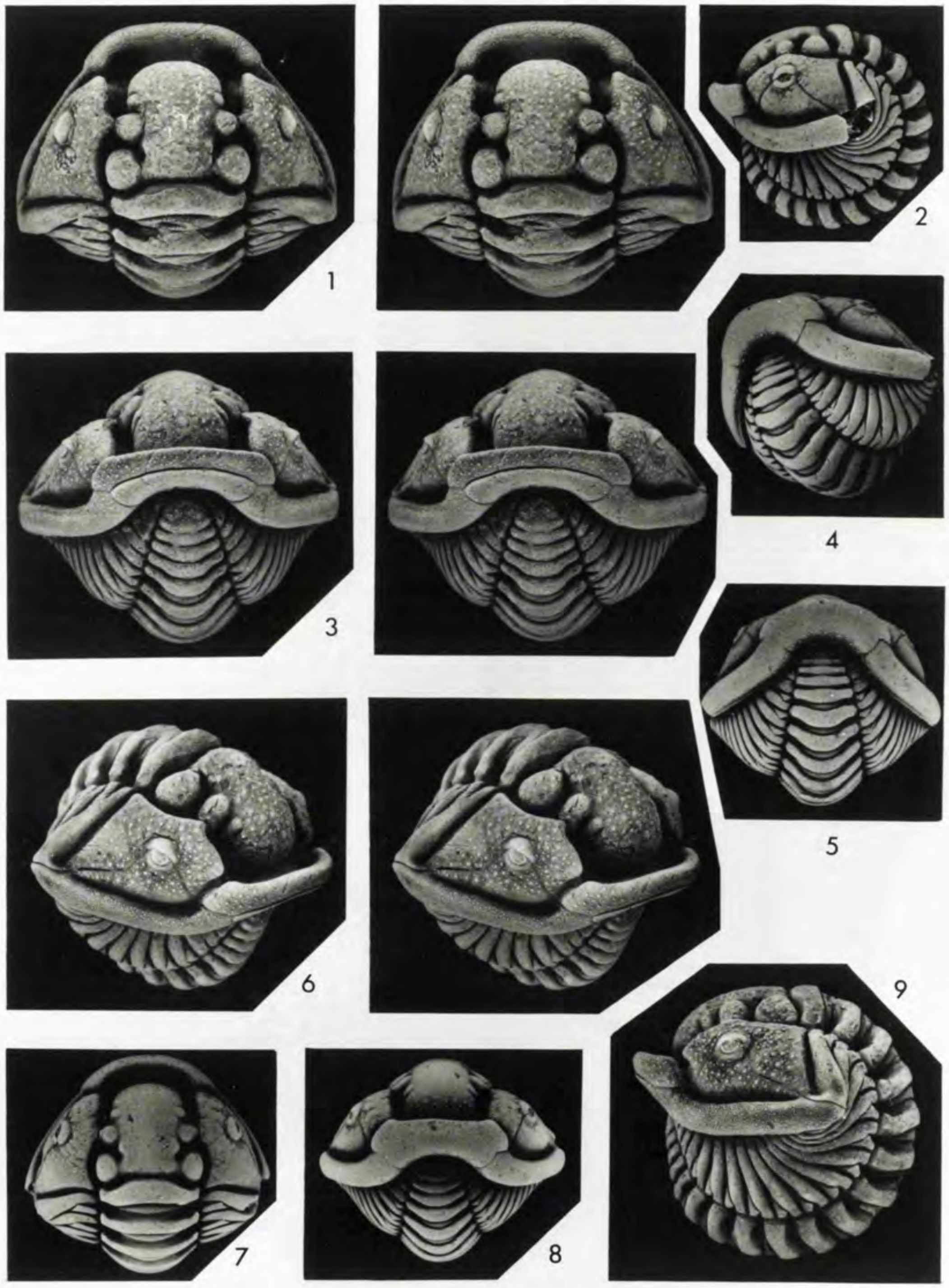

PLATE 5

Figs. 1-9. *Calymene* sp. nov.?

1, 3, Complete enrolled specimen, RM Ar27042, Visby Beds,
6, 9. Visby Hamn, Gotland. Dorsal, frontal, left oblique stereo-pairs, left lateral view, x $2\frac{1}{2}$. See also Pl. 6, figs. 1, 3.

2, 4, Complete enrolled specimen, RM Ar27048, Visby Beds,
5, 7, Norderstrand, Visby, Gotland. Left lateral, ventral-
8. oblique, left dorsal oblique, frontal, dorsal stereo-pairs, x $2\frac{1}{2}$.

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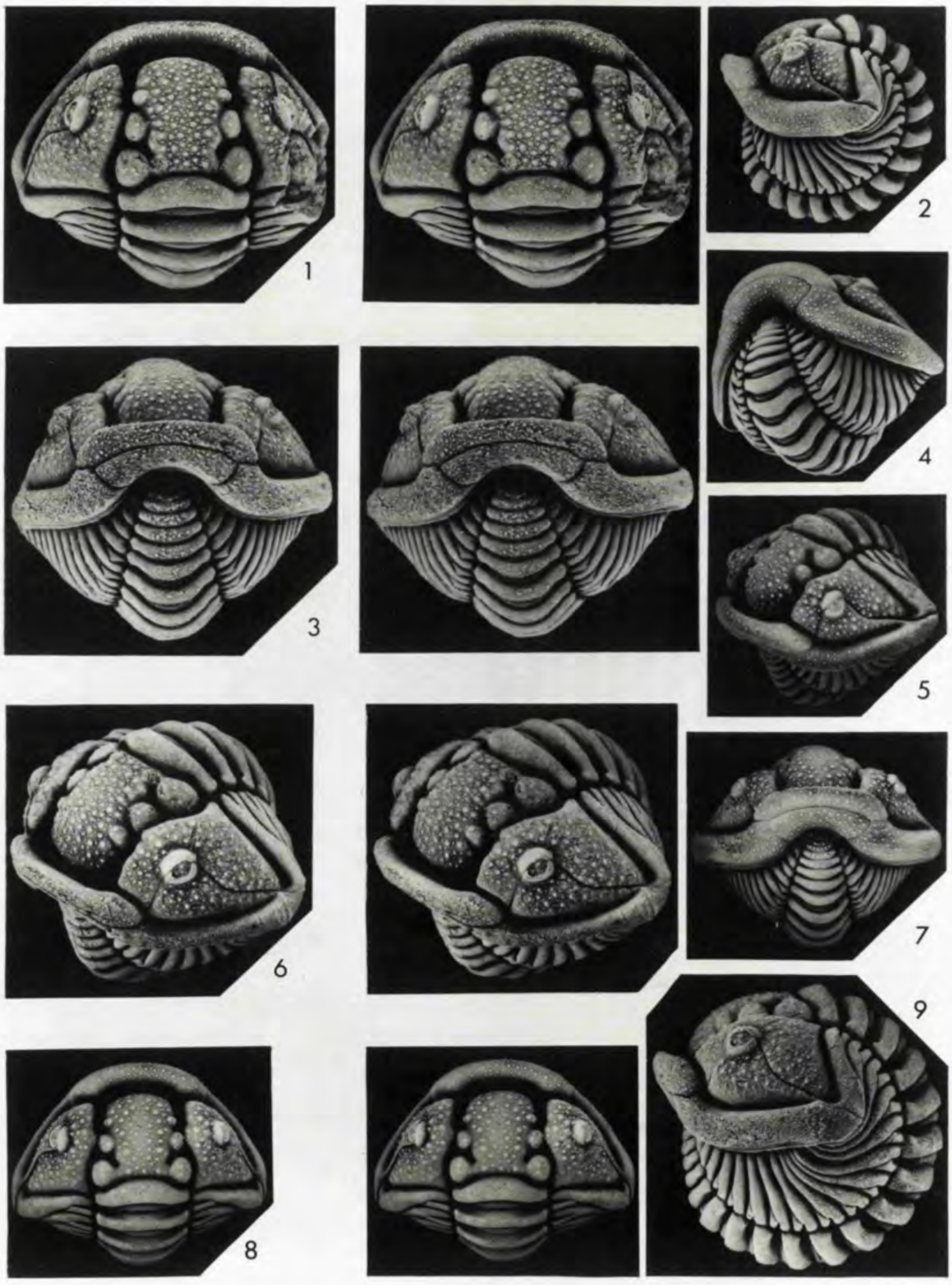

PLATE 6

Figs. 1-8. Calymene sp. nov.?

1, 3. Complete enrolled specimen, RM Ar27042, Visby Beds, Visby Hamn, Gotland. Ventral stereo-pair of rostral plate, dorsal stereo-pair of thorax, x 2½. See also Pl. 5, figs. 1, 3, 6, 9.

2, 7. Incomplete specimen, RM Ar47862. Label information reads "Hablingbo, Gotland"; this information is probably incorrect - see type stratum and type locality of C. eximia sp. nov. Dorsal view, x 2; ventral view of rostral plate, x 5.

4, 6, 8. Complete specimen, RM Ar27060, Visby Beds, Norderstrand, Visby, Gotland. Dorsal view, x 1; oblique view of pygidium, x 3; posterior view, x 2.

5. Hypostome of almost complete specimen, RM Ar27073, Visby Beds, Visby Gotland. Ventral stereo-pair, x 4.

6

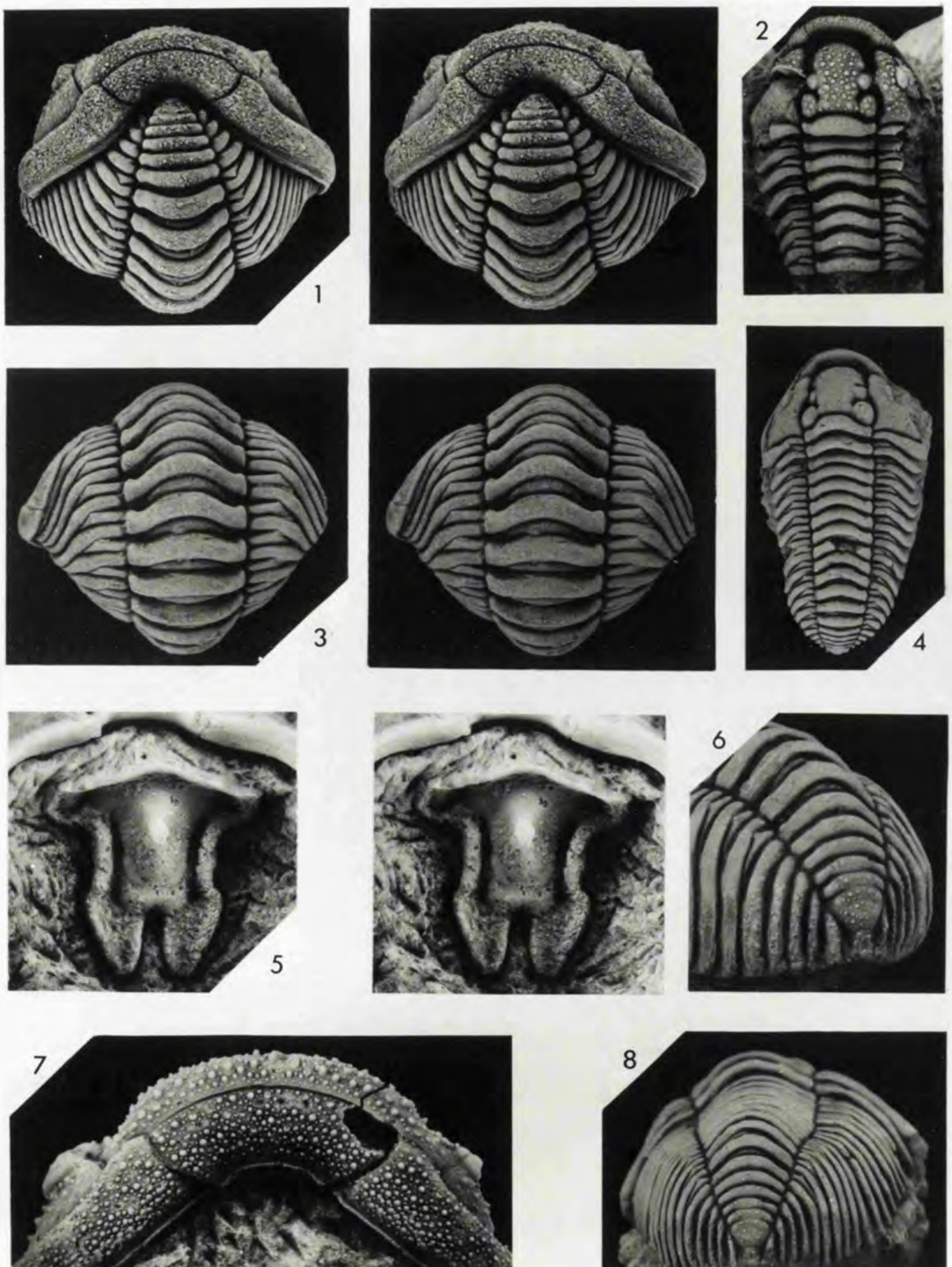

PLATE 7

Figs. 1-7. Calymene carlops Lamont, 1949

1, 2. Incomplete cranidium, 'Silcoset' rubber cast of external mould, J Ti 107d, Upper Llandovery (Telychian Stage - approximately C_6), Pentland Hills. Dorsal stereo-pair, x 4; left oblique view, x 3.

3, 4, 6, 7. Syntype, incomplete cranidium, internal mould, RSM 1956. 15. 52 (formerly Lamont Colln. 34), Plectodonta aff. canastonensis siltstones, Upper Llandovery, Deerhope, N Esk Inlier, Pentland Hills. Dorsal, right oblique, frontal, right lateral views, x 3½. Figured Lamont 1949, pl. 18, fig. 13.

5. Pygidium, internal mould, RSM 1876. 42. 60 - John Henderson Colln., same horizon and locality as for fig. 3. Posterior view, x 7. Figured Lamont 1949, pl. 18, fig. 19.

Figs. 8, 10, 11, 15. Calymene hadyardensis? Lamont, 1949

Almost complete disarticulated specimen, cuticle remaining on front part of glabella, left fixed cheek, preglabellar area, and pygidium, RSM 1956. 15. 54 (formerly Lamont Colln. 33), topmost Fronian or Telychian Stage , Penwhapple Gorge, near Penkill Castle, Girvan Area. Posterior view of pygidium, x 3½; Dorsal, frontal, left lateral views, x 2. Paratype of Calymene hadyardensis Lamont, 1949. Figured Lamont pl. 18, fig. 8.

Figs. 9, 12-14. Calymene hadyardensis Lamont, 1949

Holotype, complete damaged specimen, internal mould, GIG 1521, Telychian Stage , N side of Hadyard Hill, SW of Dailly, Girvan Area. Posterior view of pygidium, x 4½; anterodorsal view, dorsal stereo-pair, right lateral view, x 2½. Figured Lamont 1949, pl.18, figs.9-12.

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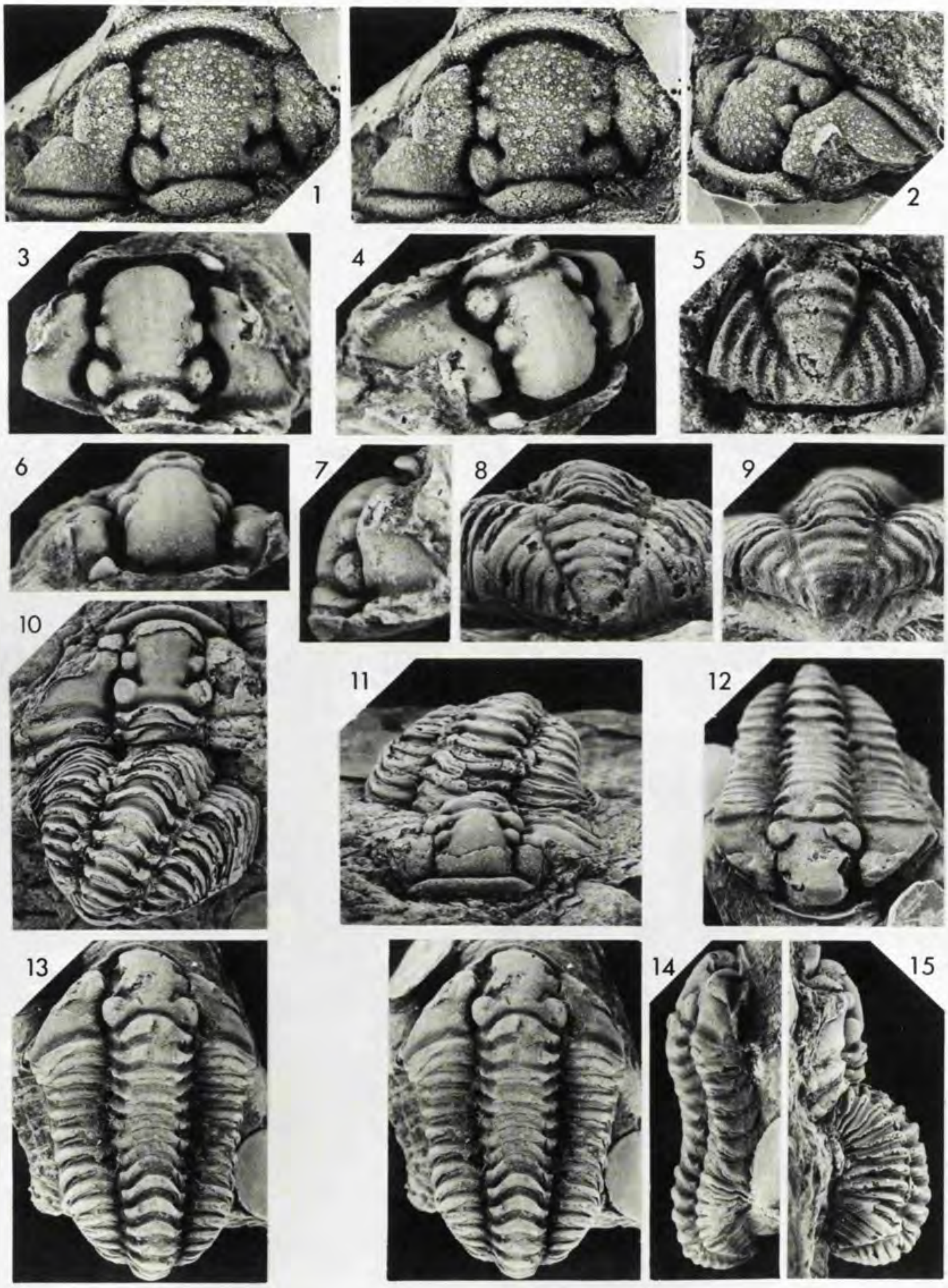

PLATE 8

Figs. 1-7. Calymene eximia sp. nov.

Holotype, incomplete cephalon with at least four attached thoracic segments, RM Ar47864, ? Hemse Beds, Hablingbo, Gotland (see discussion of type stratum and type locality). Dorsal, frontal, left oblique stereo-pairs, left lateral view, x $2\frac{1}{2}$; ventral view of rostral plate, ventral stereo-pair of hypostome, postero-ventral view of hypostome, x 5.

8

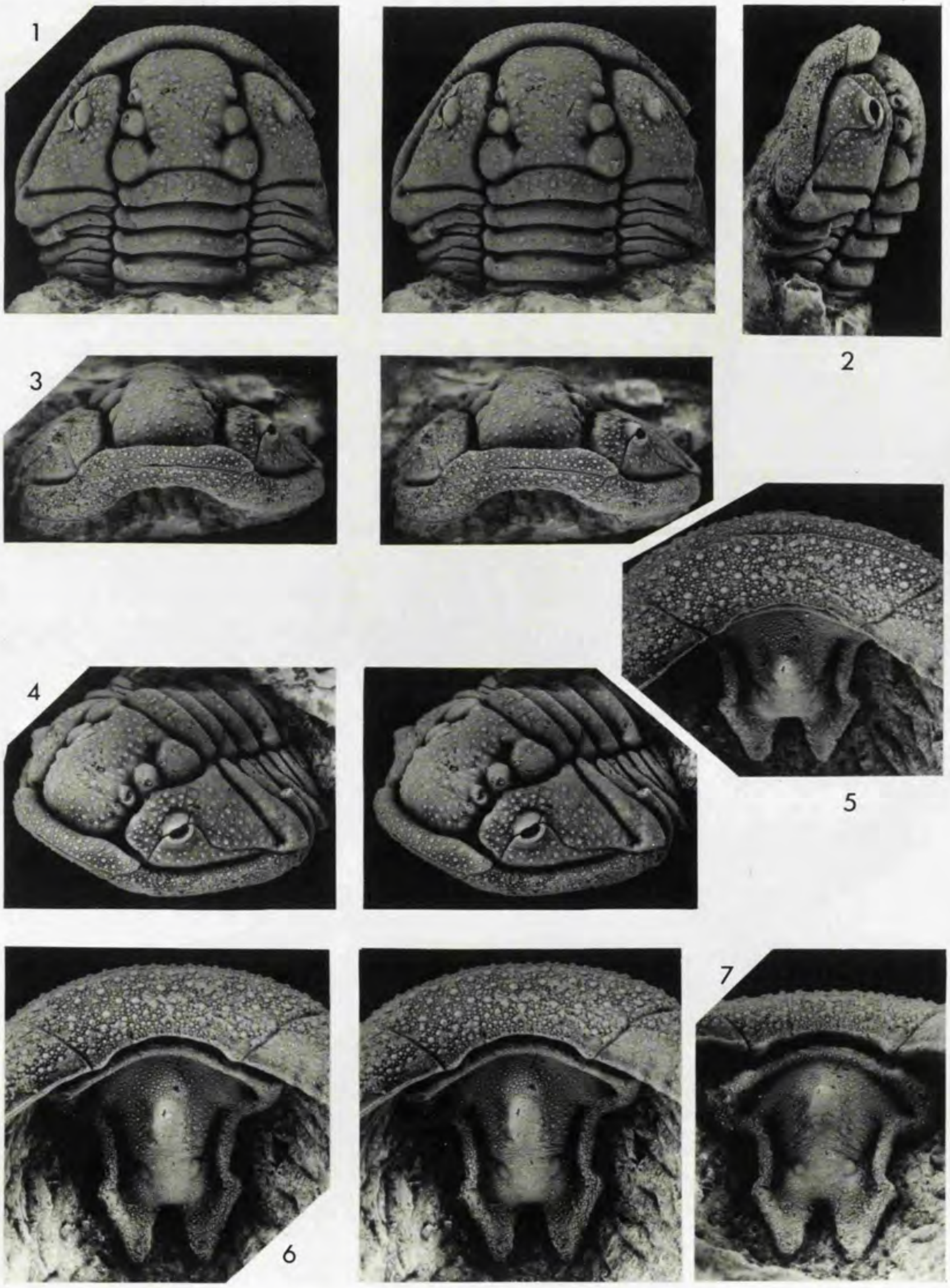

PLATE 9

Figs. 1-7. Calymene laevis Lindström, 1885

1, 3, 5-7. Lectotype, complete enrolled specimen, RM Ar6334, Västergarn, Slite Beds, Gotland. Dorsal, frontal, ventral, left oblique stereo-pairs, x 2; left lateral view, x 3. Figured Lindström 1885, pl. 16, figs. 5-7.

2, 4. Complete, partially enrolled specimen with hypostome, RM Ar27234b, Slite Beds, Västergarn, Gotland. Ventral view of hypostome which is only just visible between rostral plate and posterior margin of pygidium, x 8; dorsal view of cephalon, x 2. Original of Lindström.

9

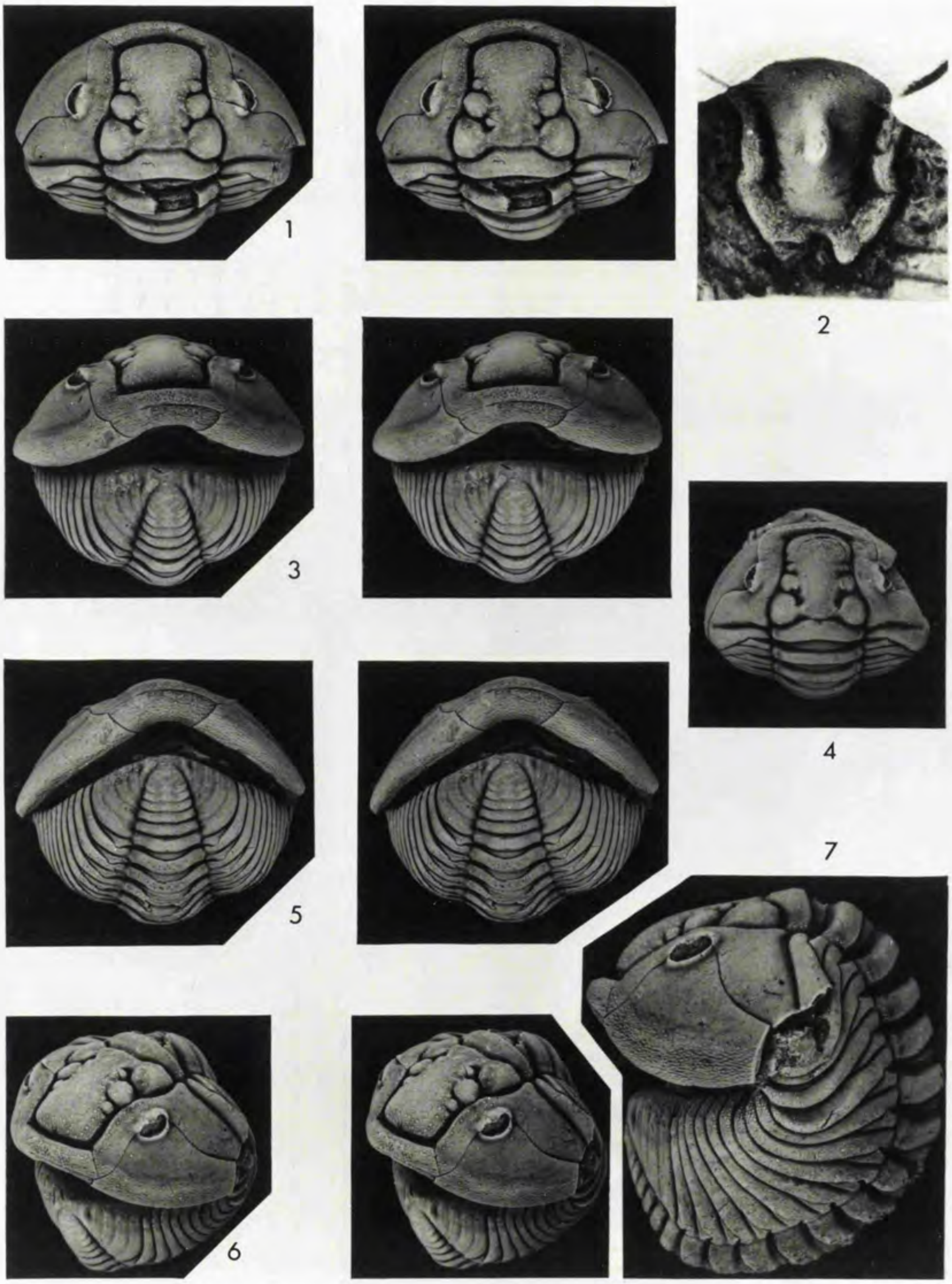

PLATE 10

Figs. 1-3. Calymene laevis Lindström, 1885

Complete enrolled specimen, RM Ar27234a, Slite Beds, Västergarn, Gotland. Dorsal (cephalon), frontal, dorsal (thorax) stereo-pairs, x 3. Original of Lindström.

Figs. 4-6. Calymene aquatica sp. nov.

Cranidium, RM Ar27300, Slite Beds, Wallstena Kanal, Gotland. Dorsal, right lateral views, x 3; right oblique view, x 2.

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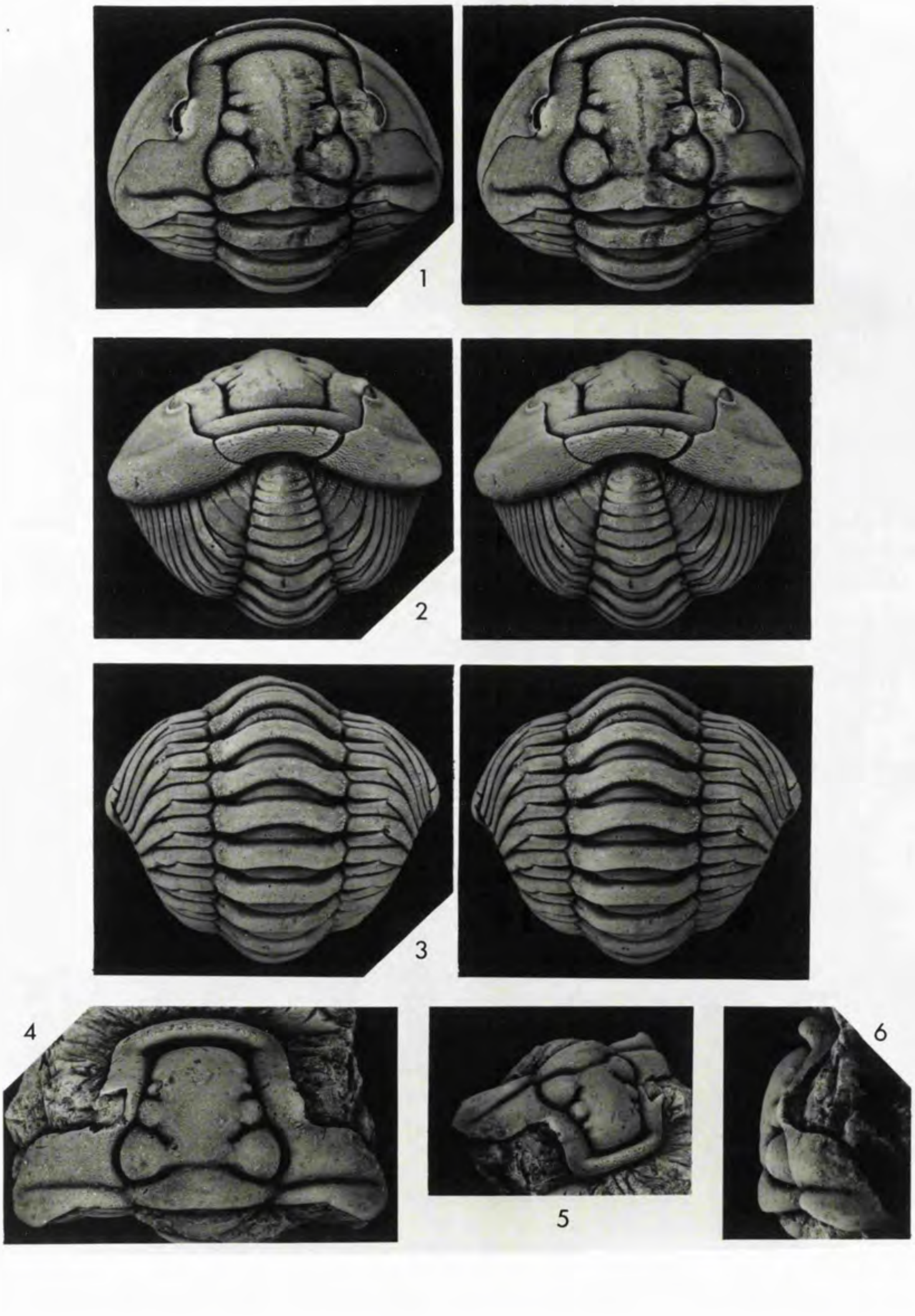

PLATE 11

Figs. 1-9. *Calymene aquatica* sp. nov.

1-4. Holotype, cranidium, RM Ar27295, Slite Beds, Wallstena Kanal, Gotland. Dorsal, frontal stereo-pairs, right oblique view, x 2; right lateral view, x 3.

5, 7-9. Cranidium, RM Ar27305, Slite Beds, Slite, Gotland. Left oblique stereo-pair, frontal view, x 2; dorsal, left lateral view, x 3.

6. Incomplete cranidium, RM Ar27289, Slite Beds, Wallstena Kanal, Gotland. Dorsal stereo-pair, x 2.

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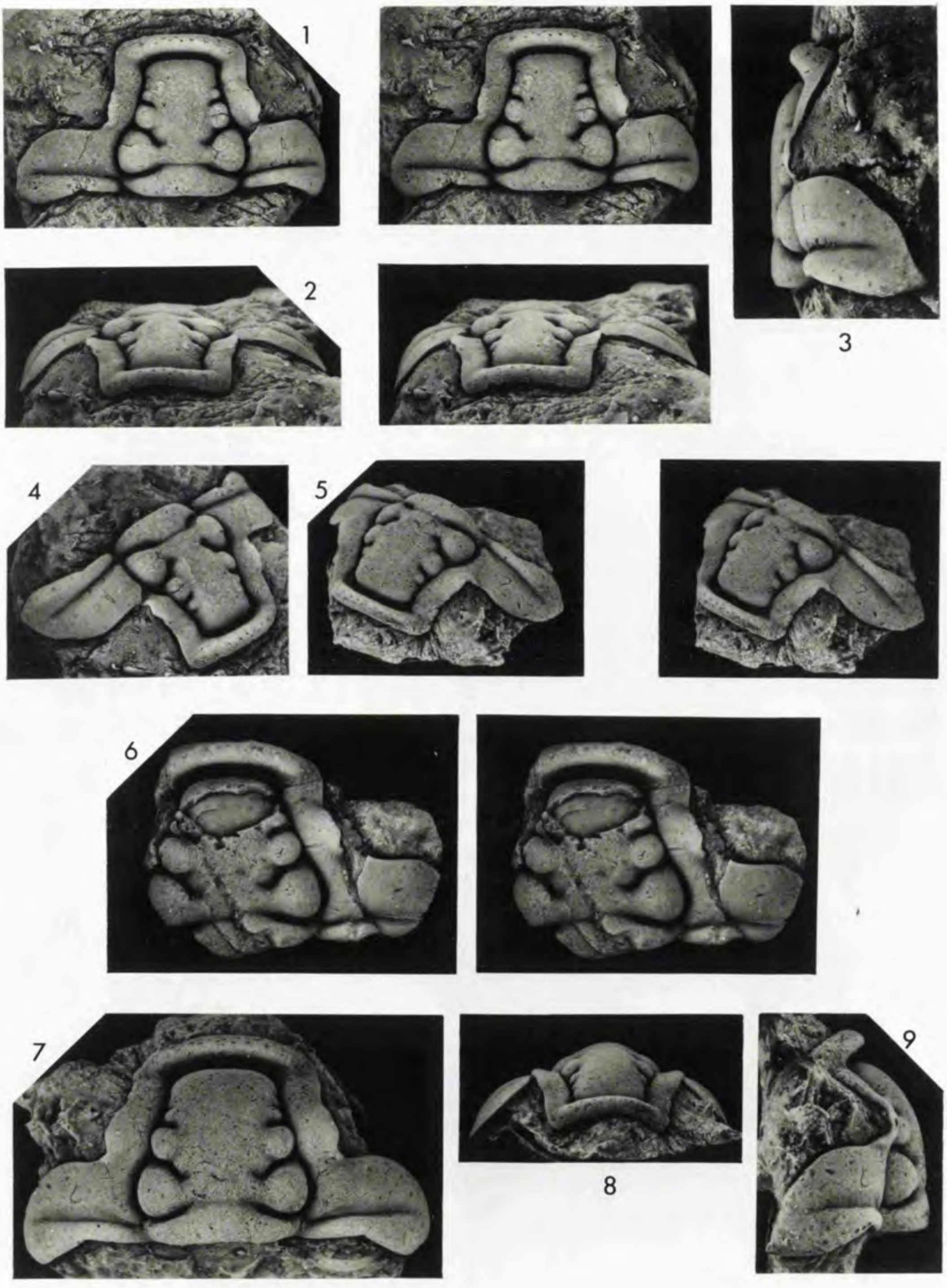

PLATE 12

Figs. 1-8. Calymene spectabilis Angelin, 1854

1-3. Incomplete cranidium, RM Ar6207, Hemse Beds, Östergarn, Gotland. Dorsal stereo-pair, right lateral view, frontal stereo-pair, x 2.

4-6. Incomplete cranidium, RM Ar27947, Hemse Beds, Sandarve kulle, Fardhem, Gotland. Dorsal, frontal views, right oblique stereo-pair, x 2.

7, 8. Incomplete cranidium, RM Ar27911, Hemse Beds, Kanalen from Visne myr, Fardhem, Gotland. Dorsal stereo-pair, left lateral view, x 2.

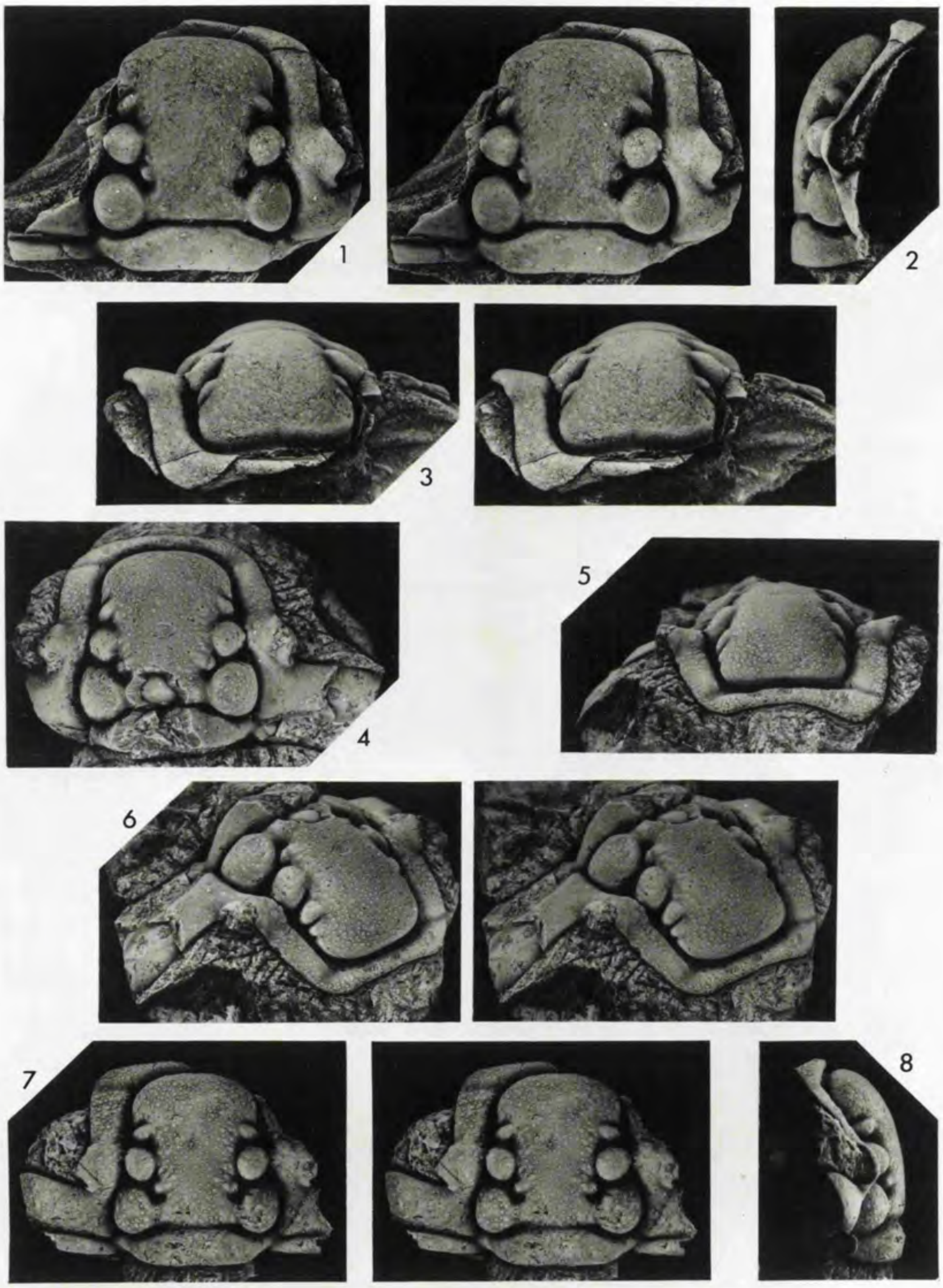
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PLATE 13

Figs. 1-10. Calymene spectabilis Angelin, 1854

1-3. Incomplete cranidium, RM Ar6208, Hemse Beds, Östergarn, Gotland. Dorsal, frontal views, x 1; right lateral view, x $1\frac{1}{2}$. Figured Schrank 1970, pl. 7, figs. 3, 3a.

4. Incomplete cranidium, RM Ar6205, Hemse Beds, Östergarn, Gotland. Dorsal stereo-pair, x 1.

5, 10. Pygidium, RM Ar31436, Hemse Beds, S of Grogarnsuvud, Gotland. Posterior stereo-pair, left lateral view, x $1\frac{1}{2}$. Figured Schrank 1970, pl. 7, figs. 5, 5a, 5b.

6-8. Pygidium RM Ar27906, Hemse Beds, Kanalen from Visne myr, Fardhem, Gotland. Posterior, dorsal, right lateral views, x 2.

9. Left free cheek, RM Ar27899, Hemse Beds, Visne myr, Fardhem, Gotland. 'Dorsal' stereo-pair, x 2.

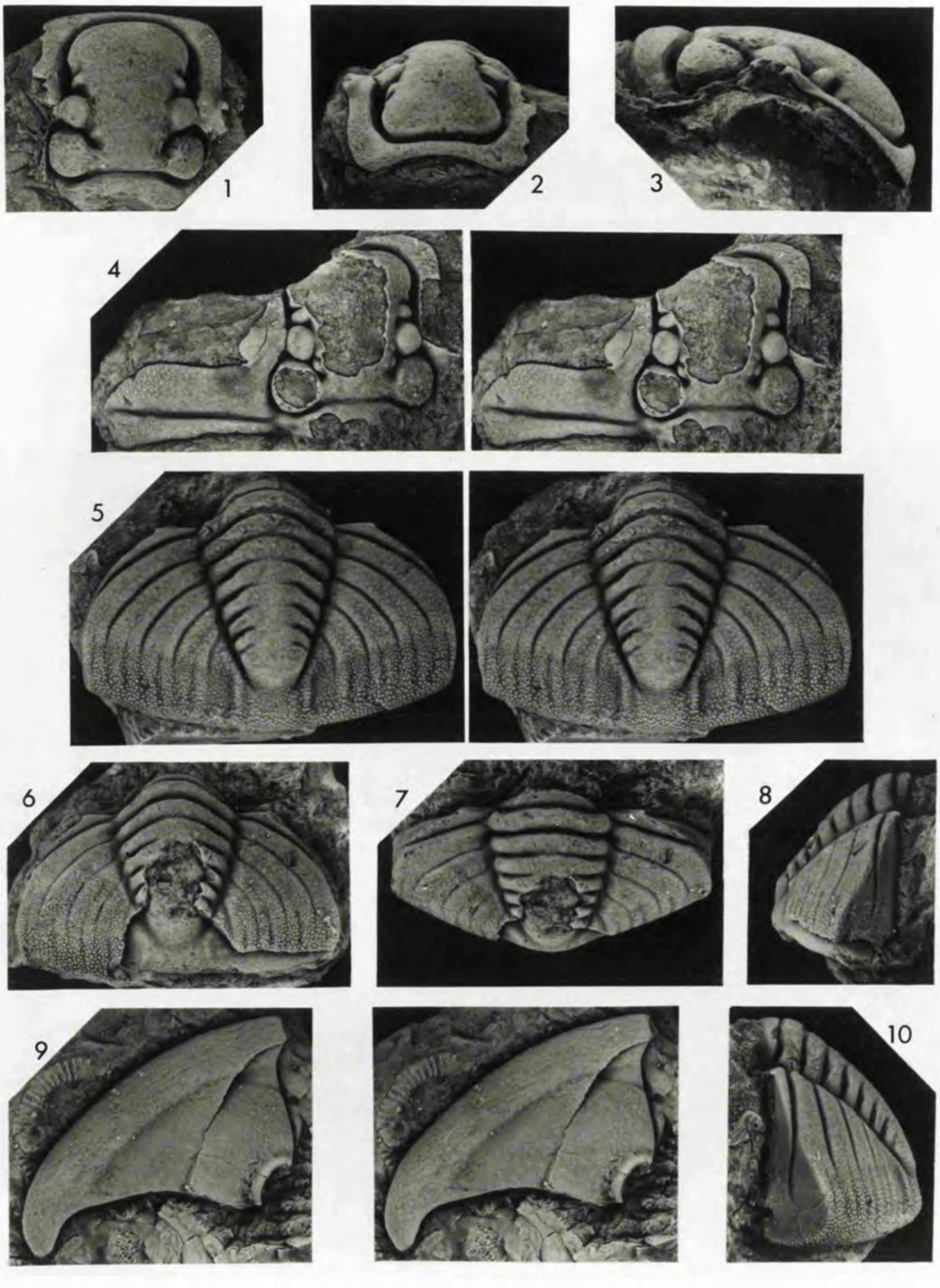
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PLATE 14

Figs. 1-3. Calymene spectabilis Angelin, 1854

1, 2. Incomplete hypostome, RM Ar46996B, Hemse Beds, Östergarn, Gotland. Ventral stereo-pair, x 2½; lateral view, x 3.

3. Incomplete hypostome, RM Ar46997b, Hemse Beds, Östergarn, Gotland. Ventral stereo-pair, x 4.

Figs. 4-8. Calymene aff. C. laevis Lindström, 1885

4, 7, 8. Incomplete cranidium, RM Ar27264, Slite Beds, Lokrumme Kanal, Gotland. Frontal view, dorsal stereo-pair, right lateral view x 3.

5, 6. Hypostome and rostral plate, RM Ar27222, Slite Beds, Eskelhem, Gotland. Ventral stereo-pair, lateral view, x 6.

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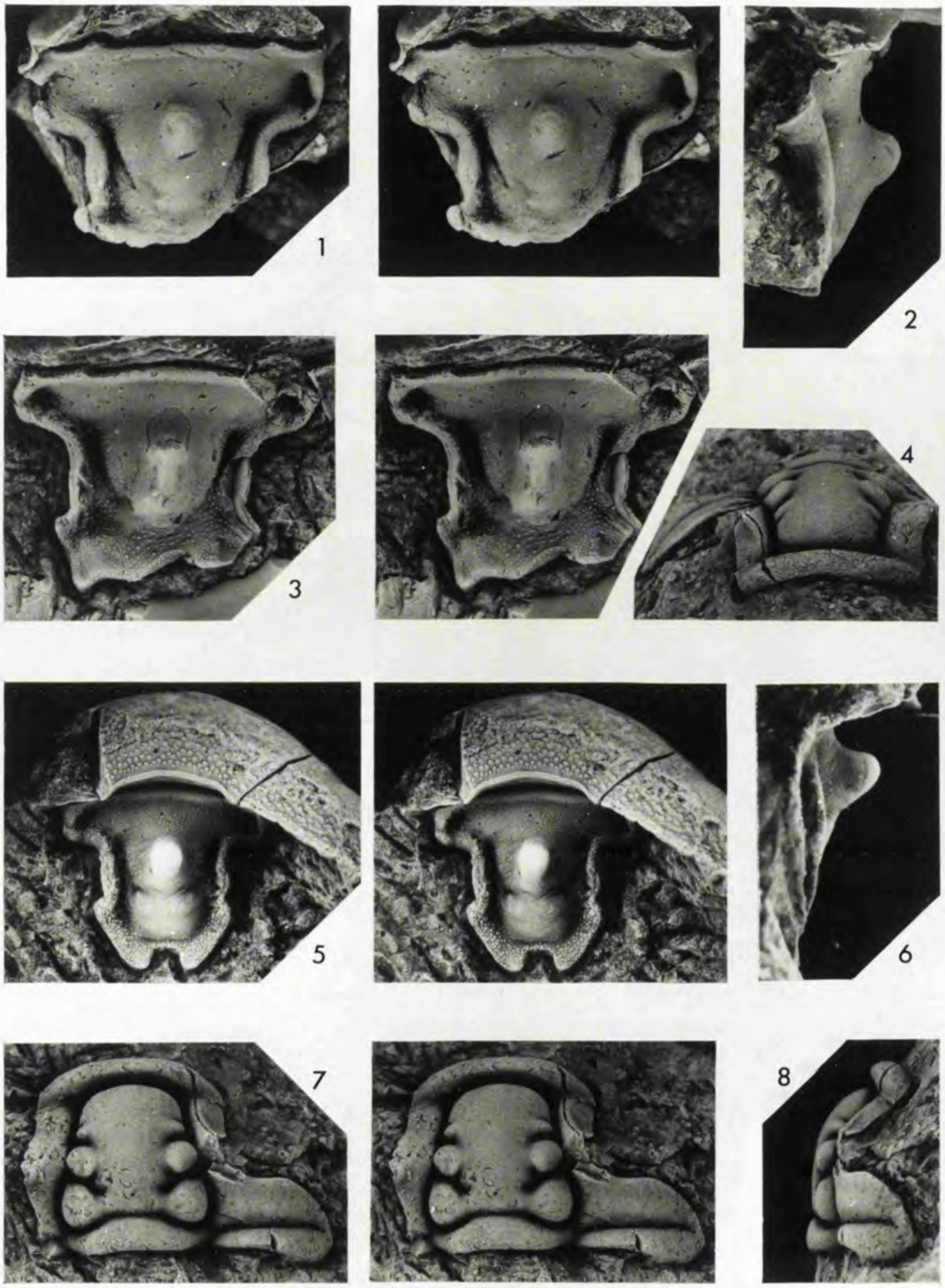

PLATE 15

Figs. 1-11. Calymene tuberculosa Dalman, 1827

1-3, 5. Incomplete cranidium, SM A84000 (formerly DJS/92), two feet above the base of the Wenlock Limestone, road section between Longville in the Dale and Stanway, Wenlock Edge. Nat. Grid. Ref. SO 53999275. Coll. R.B.Rickards. Dorsal stereo-pair, left lateral view, frontal stereo-pair, left oblique view, x 2½.

4. Right free cheek, SM A84002 (formerly DJS/94), same horizon, locality and collector as for fig. 1. 'Dorsal' stereo-pair, x 2½.

6, 10. Incomplete cranidium, SM A84001 (formerly DJS/93), same horizon, locality and collector as for fig. 1. Dorsal view, left oblique stereo-pair, x 2½. See also Pl. 17, fig. 3.

7, 11. Incomplete cranidium, RM Ar47849, Mulde Beds, Djupvik, Gotland. Dorsal view, x 2½; right lateral view, x 3.

8, 9. Thoracic segment, SM A84007 (formerly DJS/99), same horizon, locality and collector as for fig. 1. Dorsal, frontal views, x 4.

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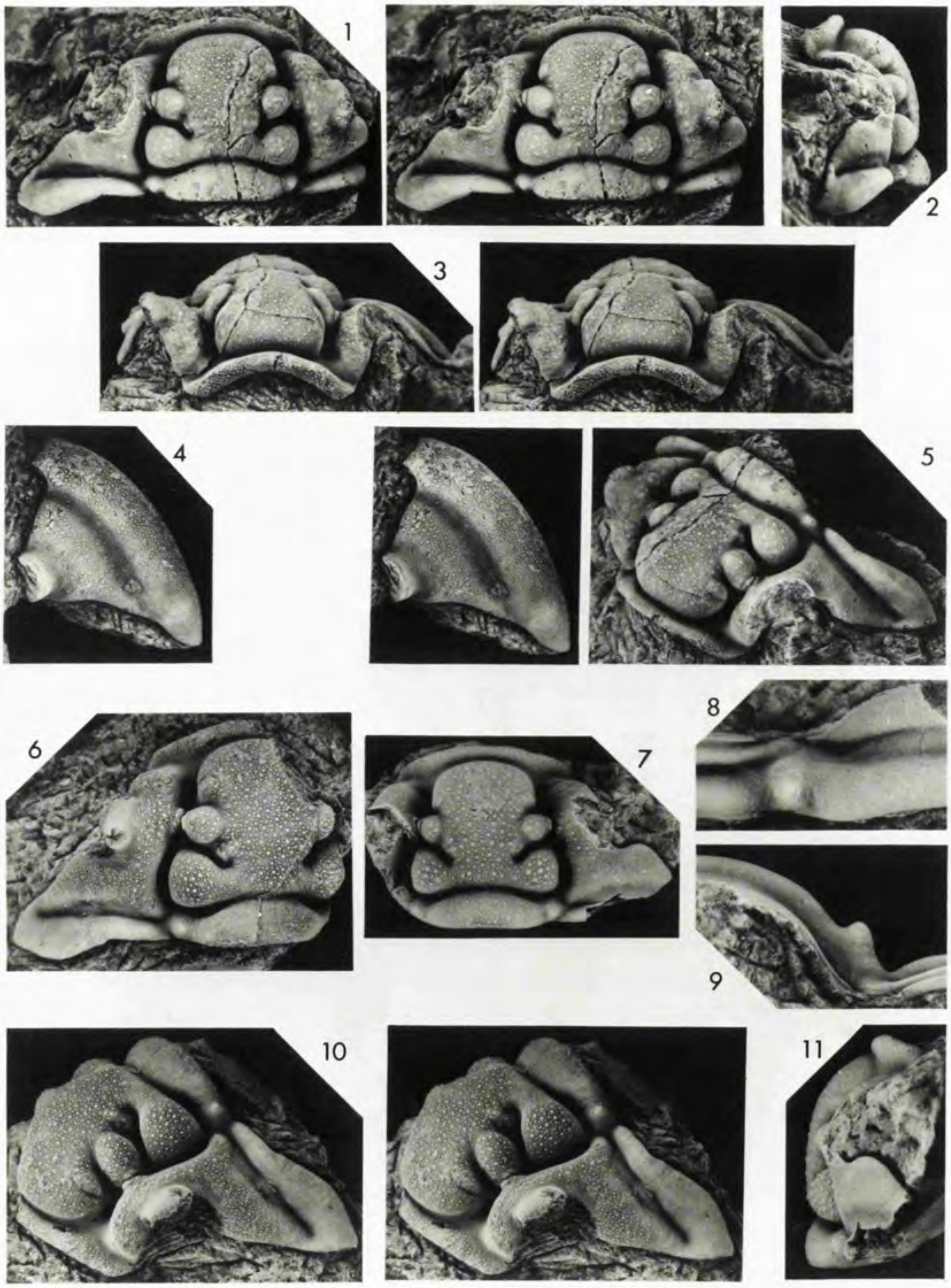

PLATE 16

Figs. 1-11. Calymene tuberculosa Dalman, 1827

1, 2, 6. Pygidium, SM A84003 (formerly DJS/95), two feet above the base of the Wenlock Limestone, road section between Longville in the Dale and Stanway, Wenlock Edge. Nat. Grid. Ref. SO 53999275. Coll. R. B. Rickards. Posterior, left oblique, left lateral views, x 8½.

3-5. Hypostome, RM Ar47851, Mulde Beds, Djupvik, Gotland. Posterior view, ventral stereo-pair, lateral view, x 5.

7, 8. Small, complete enrolled specimen, RM Ar28263, Mulde Beds, Djupvik, Eksta, Gotland. Dorsal and right oblique stereo-pairs, x 6.

9. Hypostome, RM Ar28441, Mulde Beds, Djupvik, Eksta, Gotland. Ventral view, x 8.

10, 11. Very small enrolled holaspis, RM Ar28264, Mulde Beds, Djupvik, Eksta, Gotland. Dorsal stereo-pair, x 10; right oblique view of cephalon, x 20. Note that there is no void betwaen palpebral lobe and eye socle; also lobe 2p is not in contact with fixed cheek.

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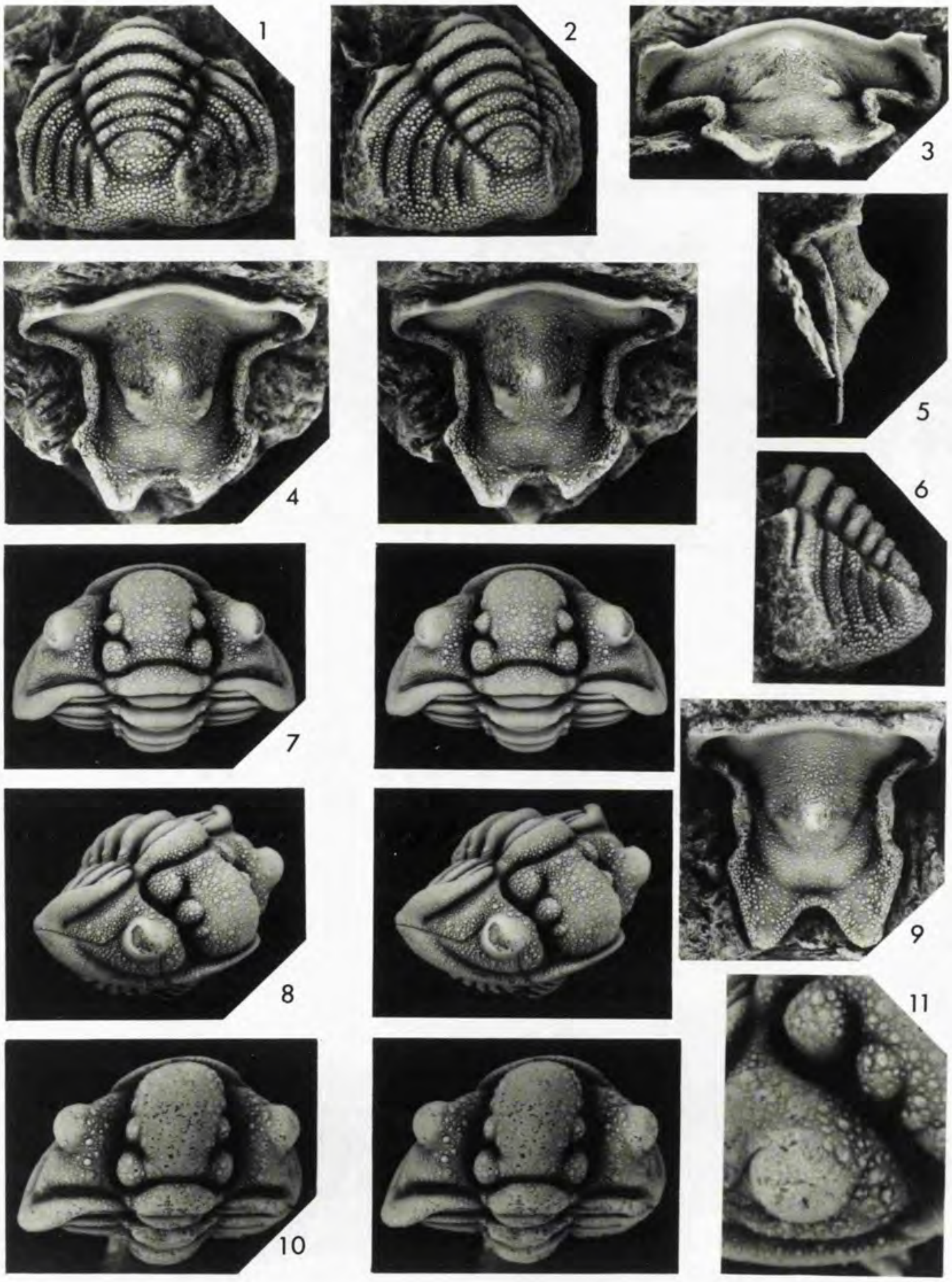

PLATE 17

Figs. 1-7. Calymene tuberculosa Dalman, 1827

1, 2, 5. Complete specimen, RM Ar47710, from Angelin's material, Silurian, Gotland (precise horizon and locality unknown). Dorsal stereo-pair, ventral stereo-pair of rostral plate, frontal view, x 2.

3. Surface ornamentation of central area of glabella, SM A84001 (formerly DJS/93), two feet above the base of the Wenlock Limestone, road section between Longville in the Dale and Stanway, Wenlock Edge. Coll. R. B. Rickards. Dorsal view, x 10. See also Pl. 15, figs. 6, 10.

4, 6, 7. Twelve thoracic segments and pygidium, RM Ar28334, Mulde Beds, Eksta, Djupvik, Gotland. Posterior and dorsal stereo-pairs, right lateral view, x 2. See also Pl. 18, figs. 1, 2.

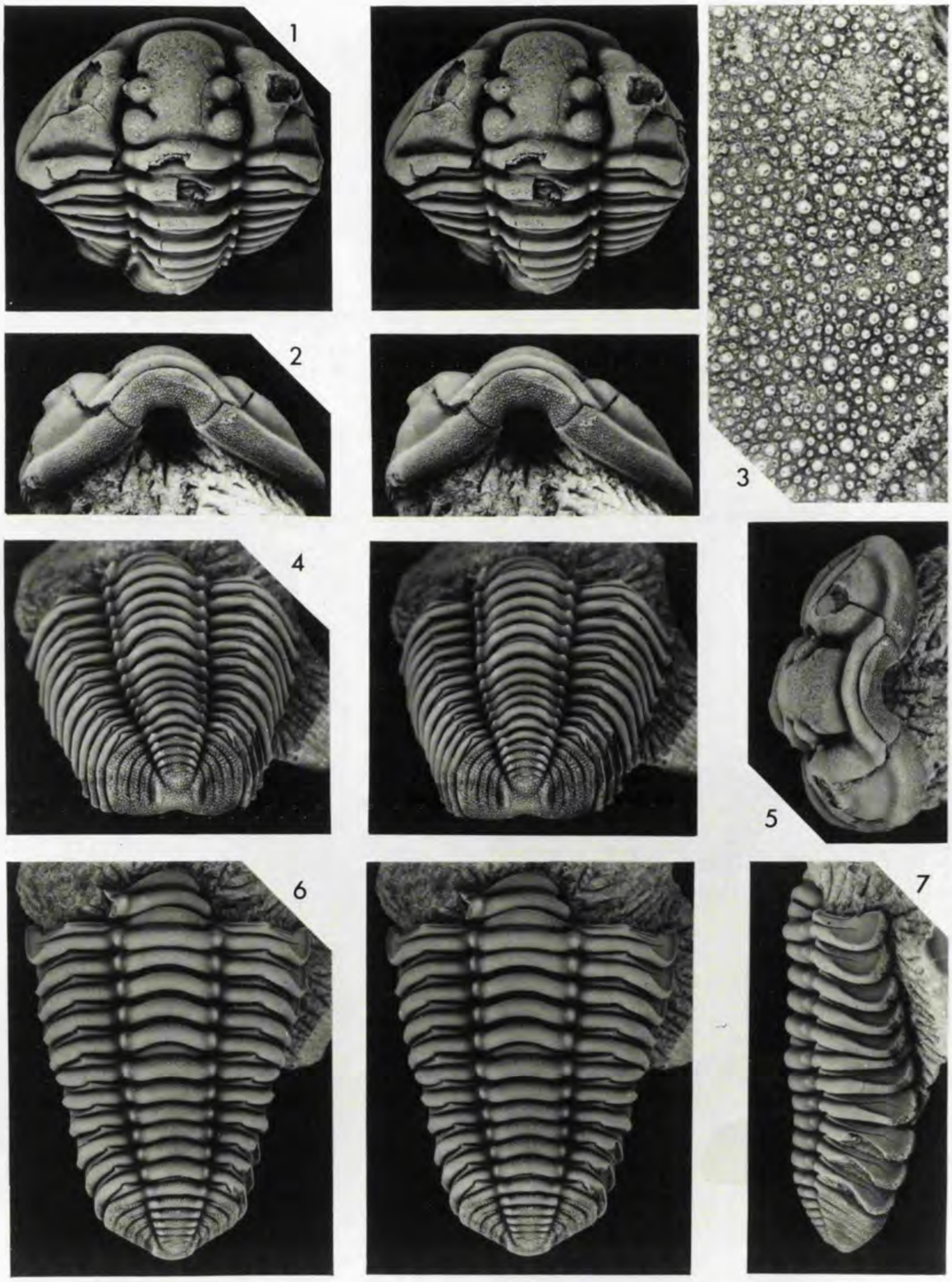
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PLATE 18

Figs. 1, 2. Calymene tuberculosa Dalman, 1827

Anterior (fig. 1) and posterior (fig. 2) thoracic pleurae, RM Ar28334, Mulde Beds, Eksta, Djupvik, Gotland. Left lateral views, x 10. See also Pl. 17, figs. 4, 6, 7. Note change in shape of posterior margin of pleurae which corresponds with change in ornamentation. This part of pleurae is in contact with border of cephalon during enrollment.

Figs. 3-8. Calymene breviceps Raymond, 1916

3, 6-8. Incomplete cephalon, DJS/103, Waldron Shale, Blue Ridge Stone Quarry, E side of Conns Creek, NE$\frac{1}{4}$ sec. 6, T. 11 N., R. 8 E., Waldron quadrangle, Shelby County, Indiana, U.S.A. Coll. D. Mikulic. Frontal and dorsal views, ventral stereo-pair of rostral plate, left lateral view, x $2\frac{1}{2}$.

4, 5. Damaged specimen lacking free cheeks and pygidium, DJS/102, same horizon, locality and collector as for fig. 3. Dorsal view, x 2; postero-dorsal view of anterior part of axis, x 9.

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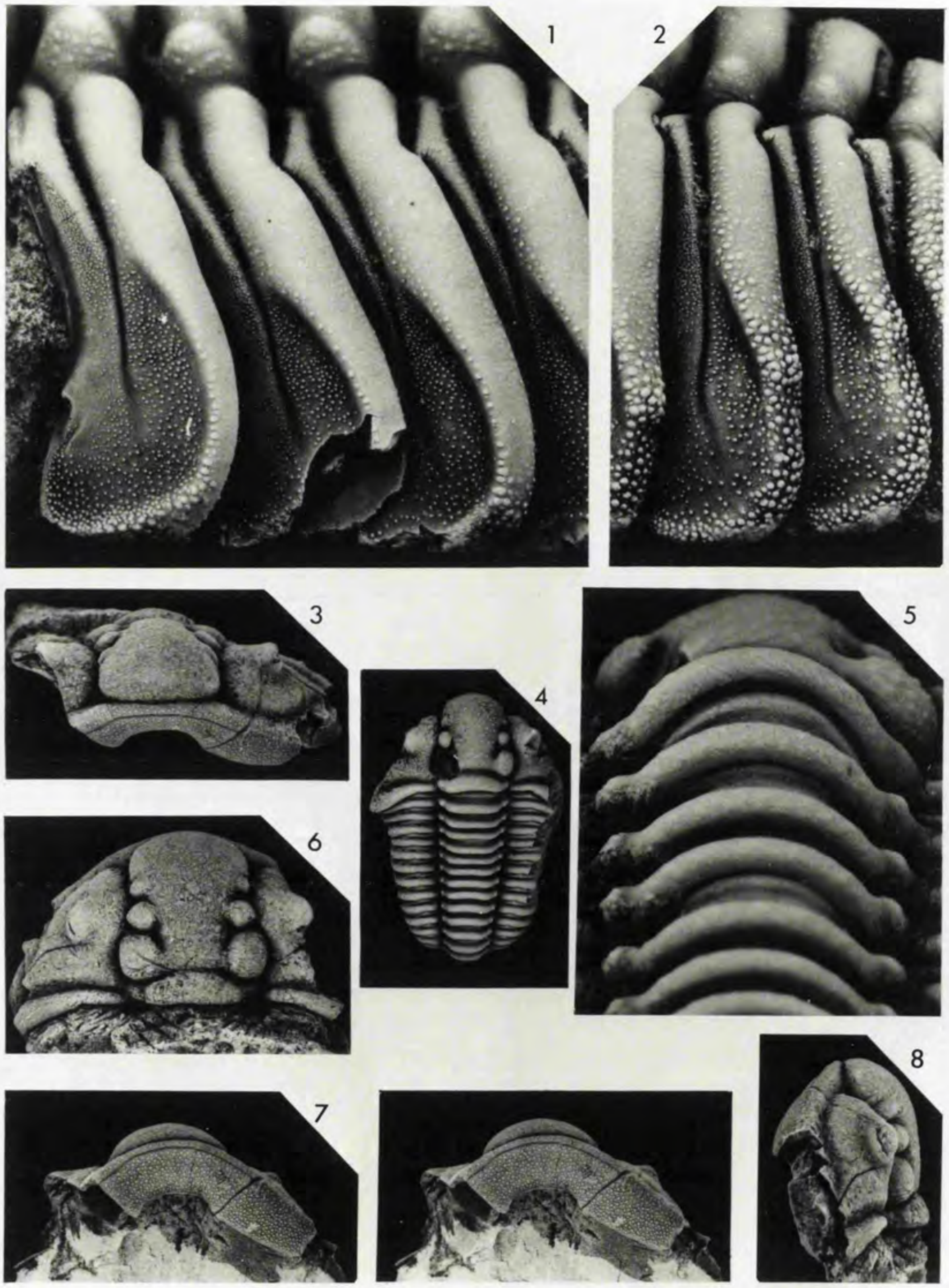

PLATE 19

Figs. 1-7. Calymene breviceps Raymond, 1916

1-3. Incomplete cranidium, DJS/100, Waldron Shale, Blue Ridge Stone Quarry, E side of Conns Creek, NE$\frac{1}{4}$ sec. 6, T. 11 N., R. 8 E., Waldron quadrangle, Shelby County, Indiana, U.S.A. Coll. D. Mikulic. Dorsal stereo-pair, left lateral view, frontal stereo-pair, x 5.

4-7. Incomplete cranidium, DJS/101, same horizon, locality and collector as for fig. 1. Dorsal stereo-pair, right lateral view, right oblique stereo-pair, frontal view, x 3.

Figs. 8, 9. Calymene interjecta Hawle & Corda, 1847

8. Right free cheek, UUG p. 5762, approximately middle part of Pridoli Formation, bed 8 at Svaty Jan, Czechoslovakia. Coll. I. Chlupac, 1966. 'Dorsal' stereo-pair, x 4.

9. Incomplete cranidium, UUG p. 5762, approximately middle part of Pridoli Formation, bed 4 at Svaty Jan, Czechoslovakia. Coll. I. Chlupac, 1966. Dorsal view, x 3.

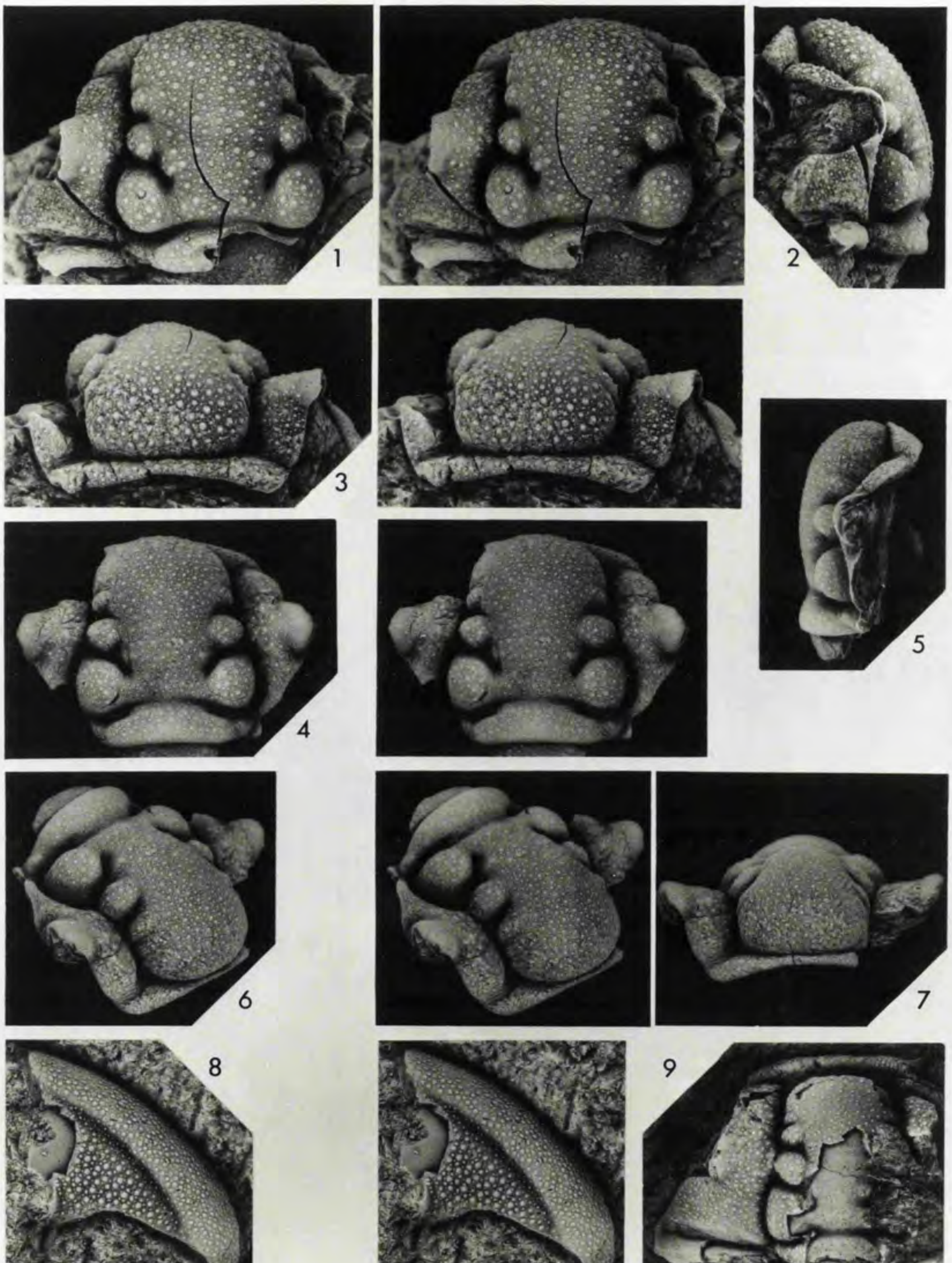
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PLATE 20

Figs. 1-9. Calymene interjecta Hawle & Corda, 1847

1, 2, 4. Incomplete cranidium, internal mould, I Ch 3953, weathered limestone, upper part of Pridoli Formation, probably zone with M. transgrediens, quarry near Pozary, near village of Reporje, SW of Prague, Czechoslovakia. Dorsal, right lateral views, right oblique stereo-pair, x $3\frac{1}{2}$.

3, 5. Pygidium, UUG p. 5762, approximately middle part of Pridoli Formation, bed 4 at Svaty Jan, Czechoslovakia. Coll. I. Chlupac, 1966. Dorsal view, posterior stereo-pair, x 3.

6. Small, incomplete cranidium with cuticle partially remaining on anterior border, I Ch 3943, same horizon and locality as for fig. 1. Dorsal view, x 8.

7-9. Incomplete cranidium, internal mould I Ch 3954, same horizon and locality as for fig. 1. Frontal and dorsal stereo-pairs, left lateral view, x 3.

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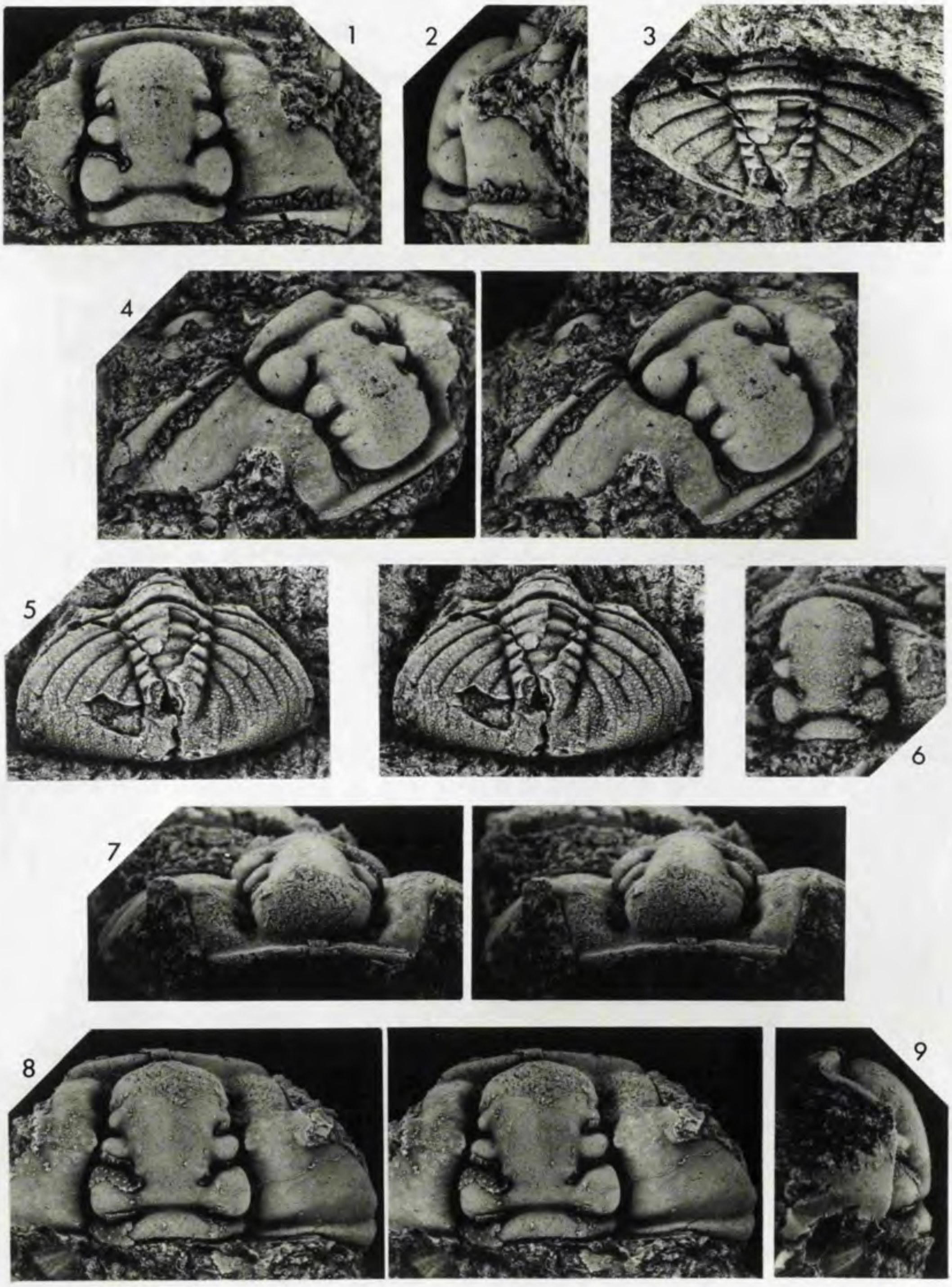

PLATE 21 (continued)

9-11. Lectotype, cast of cranidium, internal mould, NMP It 340, CF 1217, Lodenice Limestone, Lower Devonian, Luzce, Czechoslovakia. Right oblique, dorsal, left lateral views, x $1\frac{1}{2}$. Figured Barrande 1852, pl. 19, fig. 21.

PLATE 21

Figs. 1-11. Calymene interjecta Hawle & Corda, 1847

1, 2. Incomplete cranidium with cuticle partially remaining, NMW 72 29G 173, uppermost Pridoli Formation, Na brici, left bank of Berounka river above NE corner of football pitch, $\frac{1}{2}$ km N of Srbsko, Czechoslovakia. M.G.Bassett loc. CZ 37. Coll. M.G.Bassett 1972. Dorsal, frontal views, x 4.

3. Incomplete cranidium with cuticle partially remaining, NMW 72 29G 176, same horizon, locality and collector as for fig. 1. Dorsal view x $2\frac{1}{2}$. See also fig. 8.

4, 5. Pygidium, NMW 72 29G 179, same horizon, locality and collector as for fig. 1. Posterior, right lateral views, x 4.

6. Incomplete cranidium, internal mould, I Ch 3946, weathered limestone, upper part of Pridoli Formation, probably zone with M. transgrediens, quarry near Pozary, village of Reporje, SW of Prague, Czechoslovakia. Dorsal view, x $3\frac{1}{2}$.

7. Paralectotype, cast of cranidium and several attached thoracic segments, internal mould, NMP It339, CF 1218, Lodenice Limestone, Lower Devonian, Luzce, Czechoslovakia. Dorsal stereo-pair, x $1\frac{1}{2}$. Figured Barrande 1852, pl. 19, fig. 20.

8. Enlargement of anterolateral part of cranidium in top left hand corner of fig. 3, NMW 72 29G 176. x 9. Note spine-like extension of large tubercle on lateral lobe 3p.

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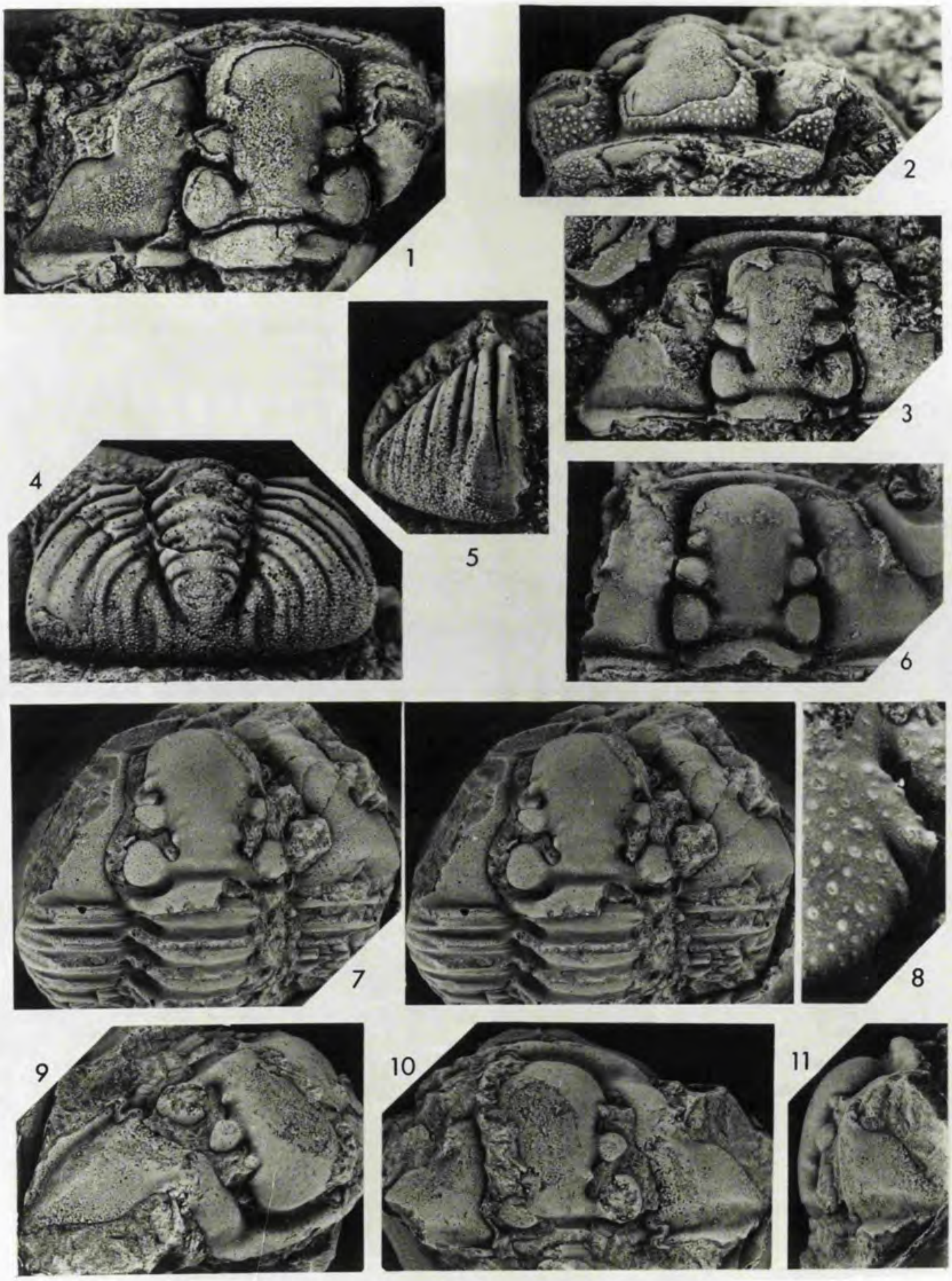

PLATE 22

Figs. 1-7. Calymene planicurvata Shirley, 1936

1, 3, 7. Incomplete cranidium, internal mould DJS/147, loose block of Bog Quartzite, Llandovery Series, Idwian Stage, Round Hill, Shelve area, Shropshire (Nat. Grid. Ref. SO 348993). Coll. Derek J. Siveter. Dorsal, frontal stereo-pairs, left oblique view, x 1½.

2, 5. Holotype, incomplete cranidium, internal mould, GSM 19624, Llandovery Series, Idwian Stage, Bog Mine, Shelve area, Shropshire. Left lateral view, dorsal stereo-pair, x 1½. Figured Shirley 1936, pl. 30, figs. 6, 7.

4. Incomplete cranidium, internal mould, DJS/148, same horizon, locality and collector as for fig. 1. Dorsal view, x 2.

6. Pygidium, internal mould, BM I4522, same horizon and locality as for fig. 2. Posterior stereo-pair, x 1.4.

Figs. 8, 9. Calymene sp. 1

Almost complete specimen, BU Hollcroft Colln. 183, Wenlock Limestone, Dudley. Ventral stereo-pair, x 1; enlargement of distal part of thoracic segments showing panderian notches and stops to enrollment, x 4.

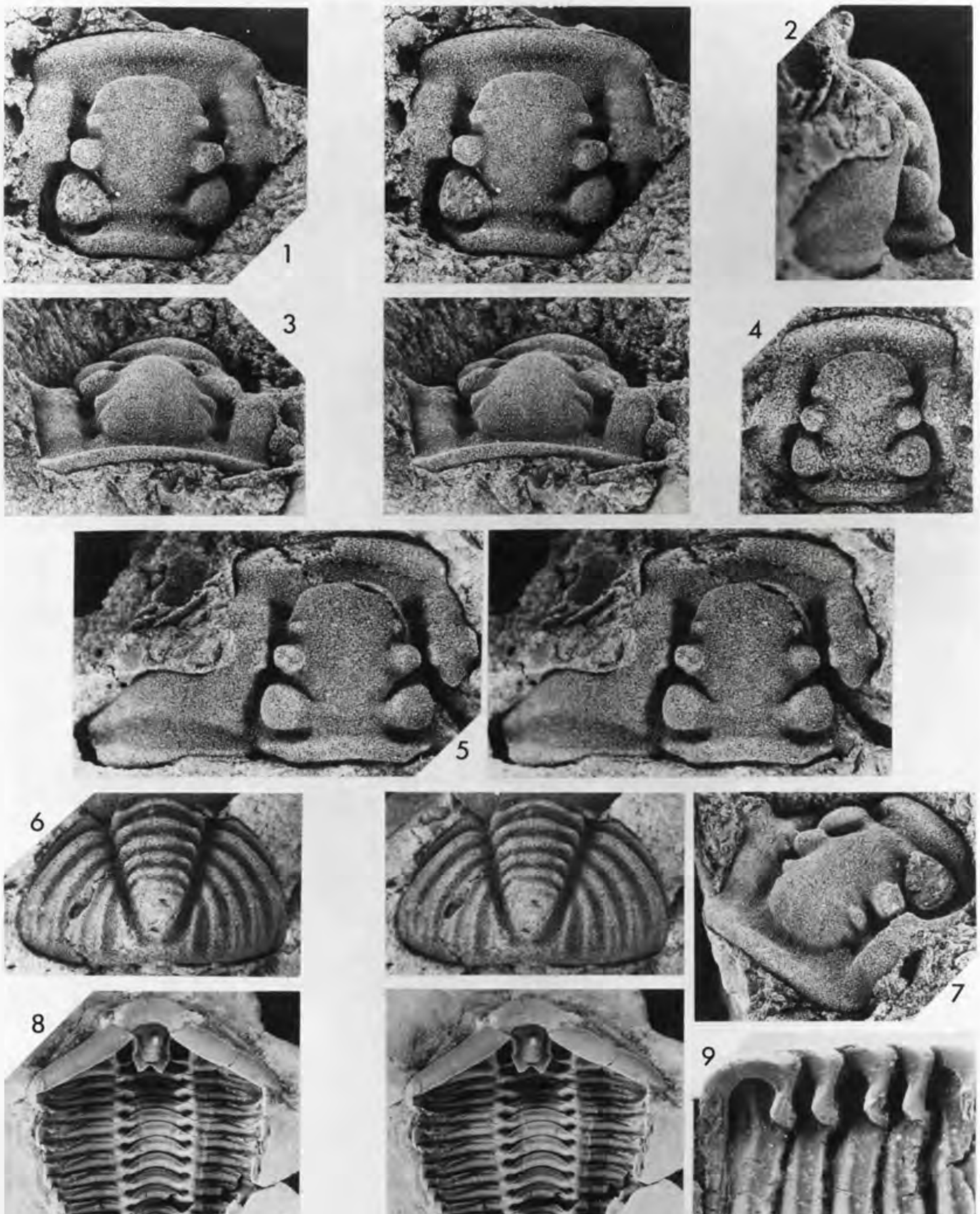
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PLATE 23

Figs. 1, 4-6. *Calymene* aff. *C. mimaspera* Schrank, 1970

Incomplete cranidium, DJS/144, cutting on the eastern bank of Harley Brook, approximately 200 yards S of junction between Harley Brook and Merrishaw Brook, near Lomas, Welsh Borderlands. Frontal, left lateral, right oblique views, dorsal stereo-pair, x 2. Coll. David J. Siveter & P. Turner, 1971.

Figs. 2, 3, 7-9. *Calymene* cf. *C. mimaspera* Schrank, 1970

2, 3, Cranidium, BM It9147, Wenlock Limestone, Dudley. Frontal,
8, 9, dorsal, right oblique stereo-pairs, x 2; left lateral view, x $2\frac{1}{2}$.

7. Incomplete cranidium, RSM 1911. 62. 1689 (Neilson Colln.), Wenlock Limestone, Dudley. Dorsal stereo-pair, x 2.

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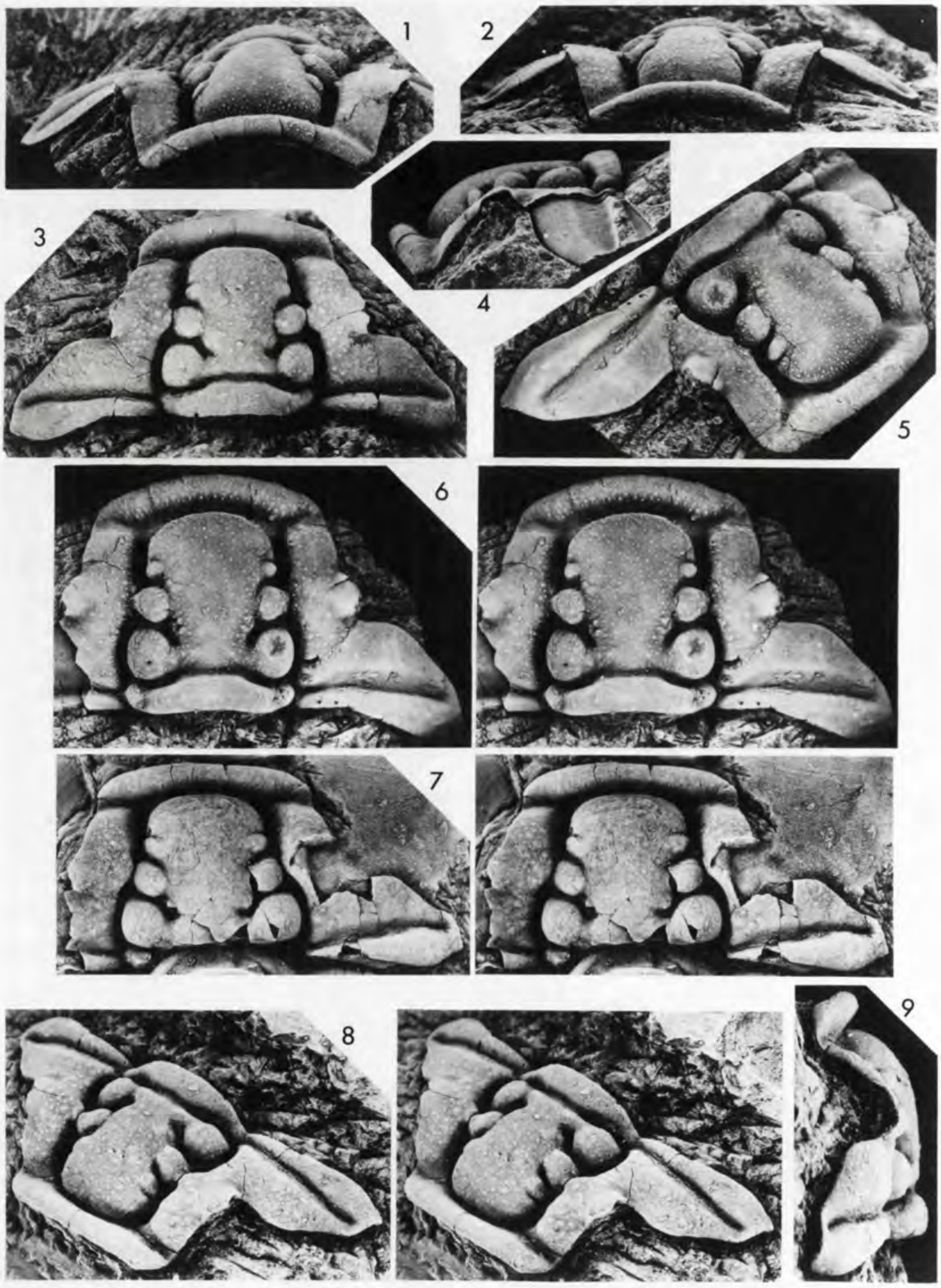

PLATE 24

Figs. 1-7. Calymene aspera Shirley, 1936

1-3, 6. Holotype, complete specimen, BM In28659, Wenlock Limestone, Dudley. Dorsal stereo-pair of cephalon, right oblique view, dorsal stereo-pair of thorax, ventral stereo-pair, x $2\frac{1}{2}$. Figured Shirley 1936, pl. 30, figs. 8-10.

4. Almost complete cranidium and several thoracic segments, internal mould, BM 44322, Wenlock Series, Penylan Quarry, near Cardiff. Coll. E. E. Kirby. Dorsal view, x 2.

5. Complete enrolled specimen, BM In28658, Wenlock Limestone, Dudley. Dorsal view, x 2.

7. Cranidium, internal mould, NMW 40. 199. G2. 3, Wenlock Series, Penylan Quarry, near Cardiff. Dorsal view, x 2.

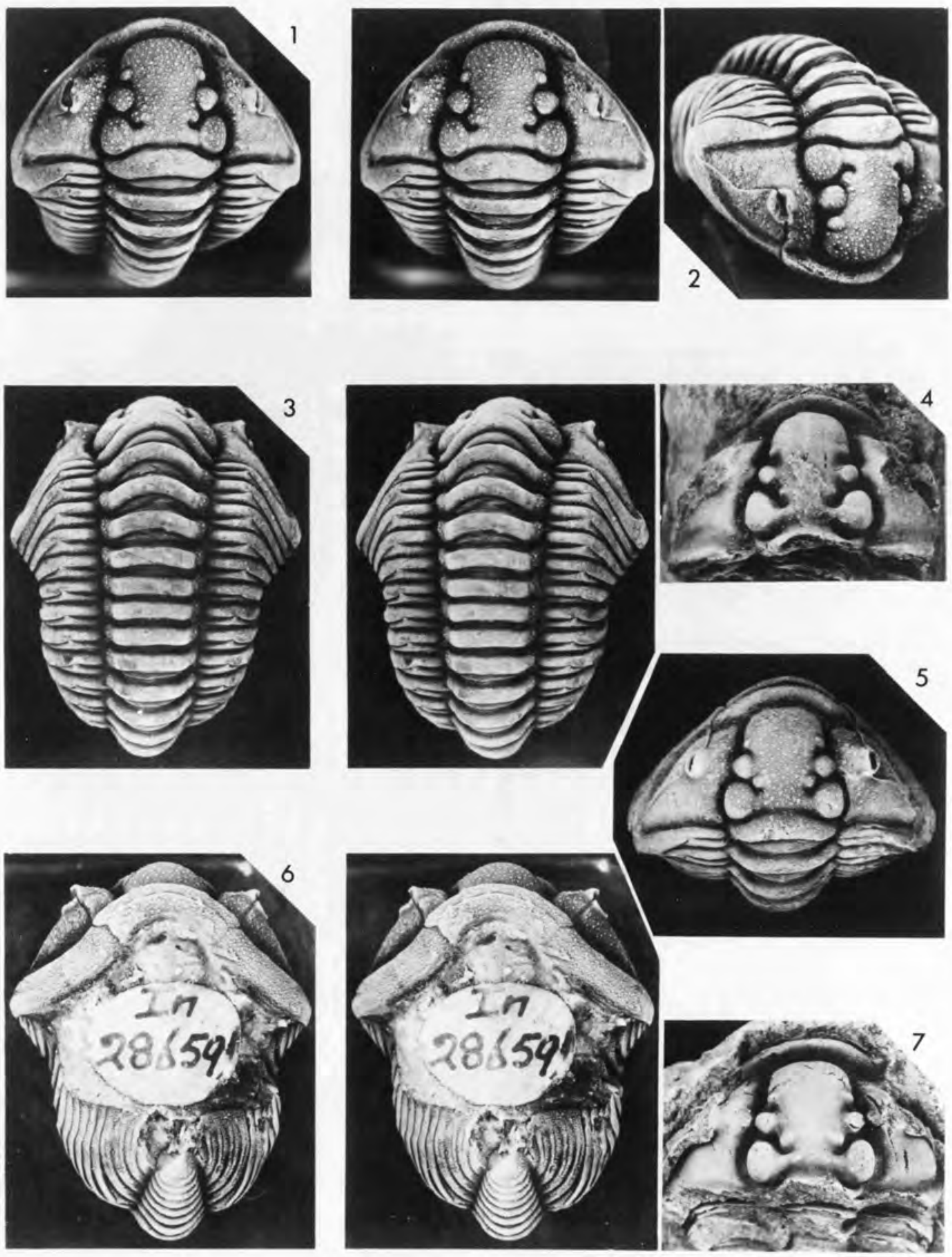

PLATE 25

Figs. 1-6. Calymene aspera Shirley, 1936

1-4, 6. Complete, partially enrolled specimen, BM In28653, Wenlock Limestone, Dudley. Dorsal stereo-pair of cephalon, left lateral view, left oblique and frontal stereo-pairs, dorsal view of thorax and pygidium, x 3.

5. Complete enrolled specimen, BM In28652, Wenlock Limestone, Dudley. Stereo-pair of rostral plate (ventral view) and pygidium (posterodorsal view), x 2½.

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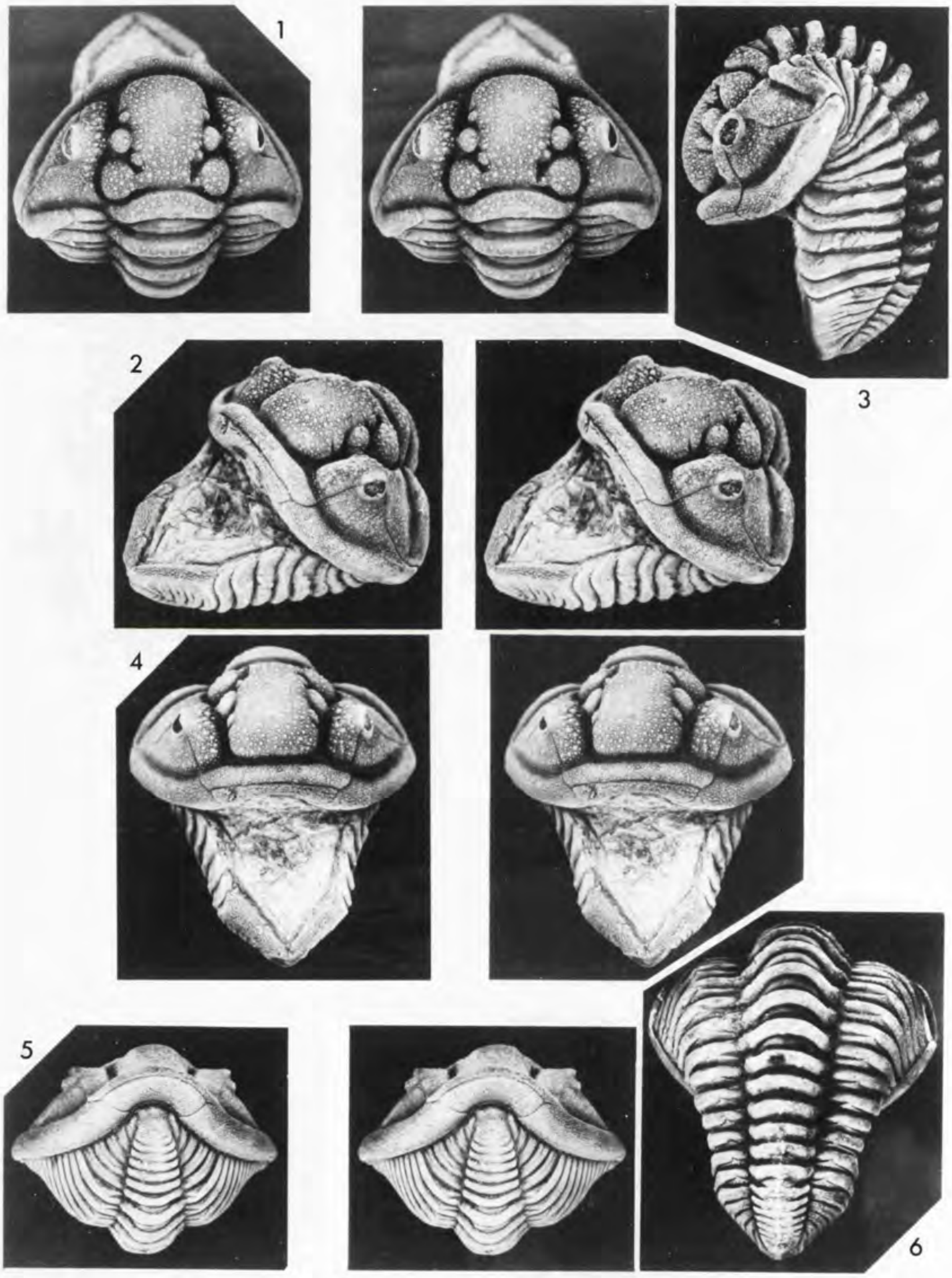

PLATE 26

Figs. 1-6. *Calymene falcata* sp. nov.

Holotype, complete specimen, RM Ar31438, Mulde Beds, Fröjel, Gotland. Dorsal stereo-pair of cephalon, left lateral view, dorsal stereo-pair of thorax, left oblique view, x $1\frac{1}{4}$; posteroventral stereo-pair of hypostome, ventral view of hypostome and rostral plate, x 3. See also Pl. 27, figs. 1, 5.

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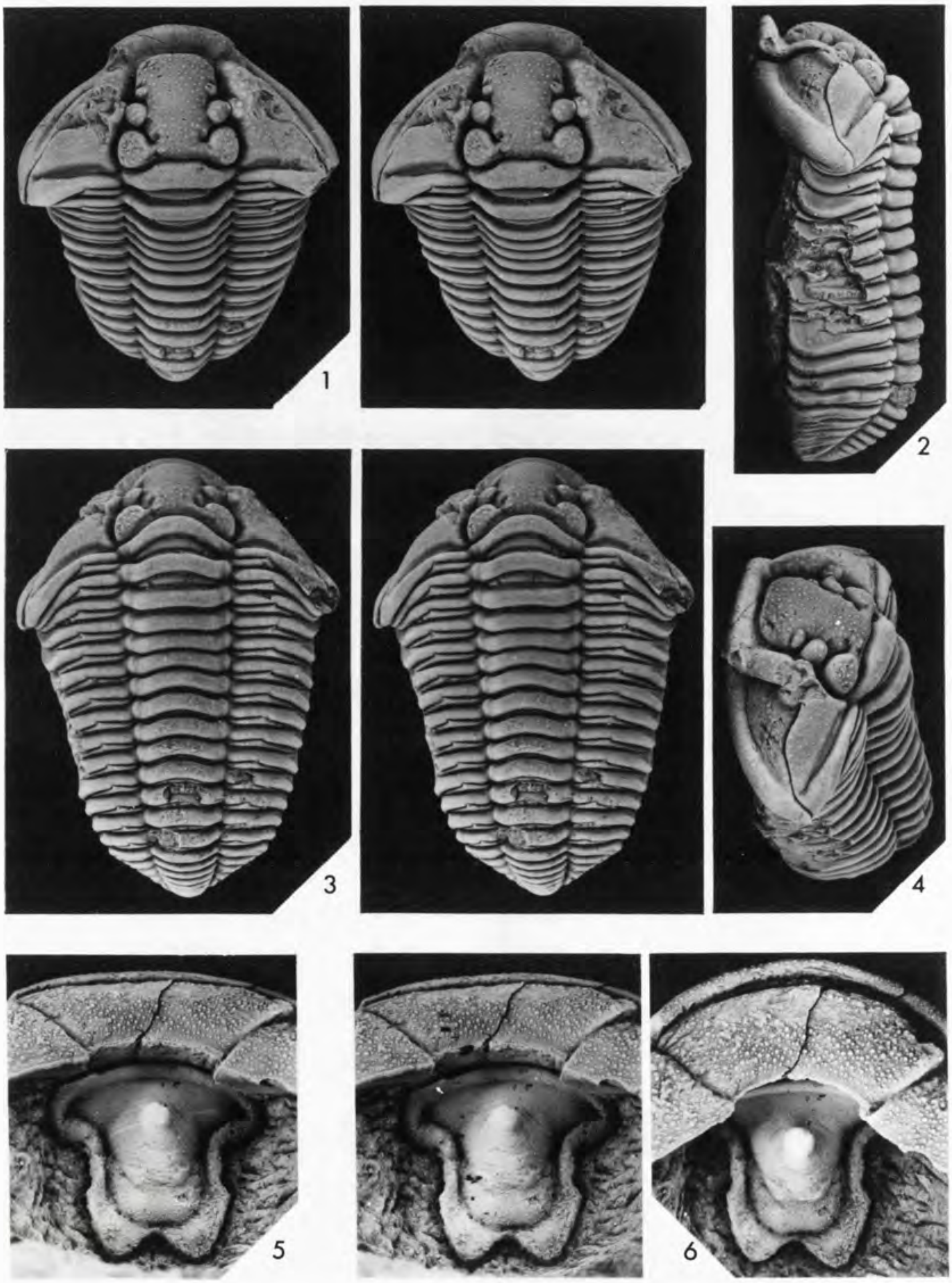

PLATE 27

Figs. 1-8. Calymene falcata sp. nov.

1, 5. Holotype, complete specimen, RM Ar31438, Mulde Beds, Fröjel, Gotland. Posterior stereo-pair of pygidium, ventral view of rostral plate, x $1\frac{1}{4}$. See also Pl. 26, figs. 1-6.

2-4, 6. Almost complete cephalon, RM Ar27376, Mulde Beds, Fröjel, Gotland. Right lateral view, dorsal stereo-pair, left oblique and frontal views, x $1\frac{1}{2}$.

7, 8. Almost complete specimen, RM Ar27379, Mulde Beds, Djupvik, Eksta, Gotland. Dorsal stereo-pair of cephalon, left lateral view, x $1\frac{1}{2}$.

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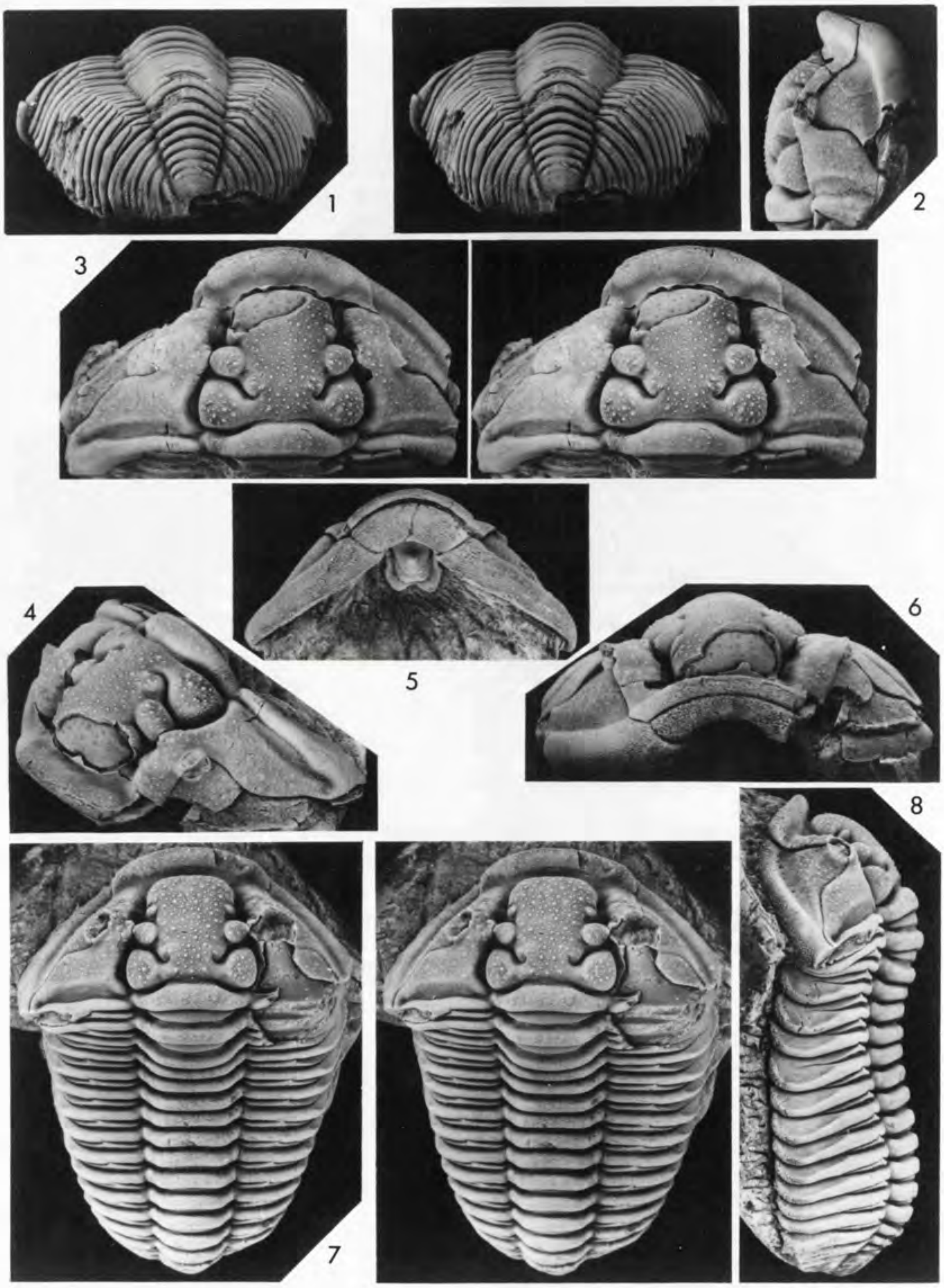

PLATE 28

Figs. 1-9. Calymene blumenbachii Brongniart, 1822

1, 3, 5, 6. Complete, partially enrolled specimen, BM 44213, Wenlock Limestone, Dudley. Dorsal and right oblique stereo-pairs, frontal and left lateral views, x 2.

2. Two specimens - one, an almost complete specimen (minus its free cheeks and pygidium), the other, an overturned cephalon, WM unnumbered, Wenlock Limestone, Dudley. Dorsal view, x $1\frac{1}{4}$. Holotype of Calymene ceratophthalma Woodward, 1868, pl. 21, fig. 1.

4, 7. Complete enrolled specimen, SM A3322, Wenlock Limestone, Dudley. Left lateral and dorsal views, x 2. Figured Shirley 1936, pl. 30, fig. 12 as Calymene lata sp. nov.

8, 9. Hypostome and rostral plate of complete specimen, BU Hollcroft Colln. 642, Wenlock Limestone, Dudley. Ventral stereo-pair, posteroventral view, x 5.

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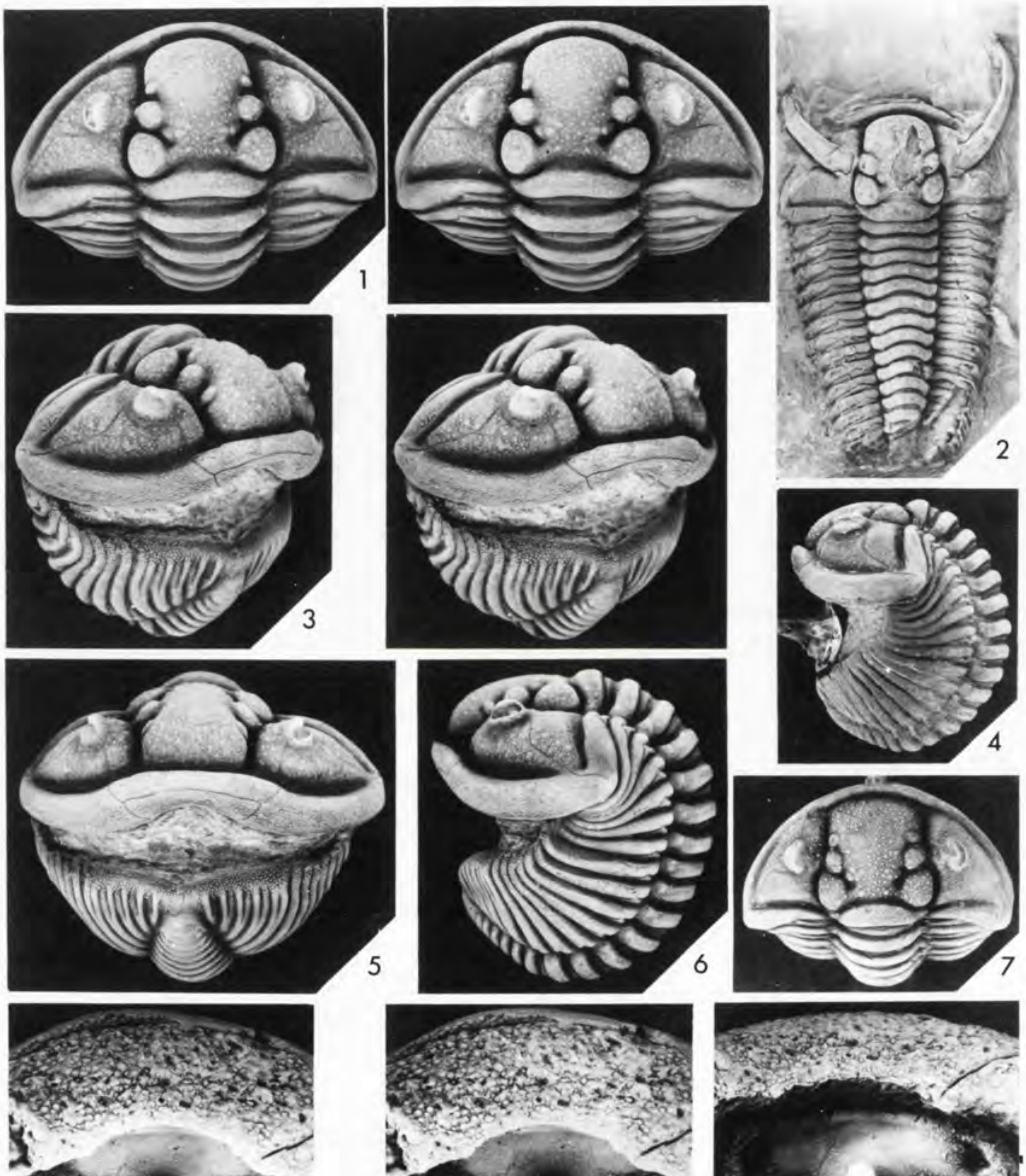

PLATE 29

Figs. 1-8. Calymene blumenbachii Brongniart, 1822

1, 3. Complete, partially enrolled specimen, BU Hollcroft Colln. 413, Wenlock Limestone, Dudley. Dorsal (cephalon) and posterior (pygidium) stereo-pairs, x 2. Note blunt outline to frontal lobe.

2, 8. Complete specimen, SM A3325, Wenlock Limestone, Dudley. Right lateral, dorsal views, x 1. Holotype of Calymene lata Shirley, 1936, pl. 30, figs. 11, 13.

4, 5. Complete, partially enrolled specimen, GSM 19668, Wenlock Limestone, Dudley. Dorsal view of thorax, left oblique view of cephalon, x 2. Figured Shirley 1933, pl. 1, fig. 4 as C. blumenbachii. See also Pl. 30, figs. 1-3.

6, 7. Complete enrolled specimen, BU Hollcroft Colln. 283, Wenlock Limestone, Dudley. Dorsal, left lateral views, x 2. Outline of frontal lobe intermediate between that of fig. 3 (above) and Pl. 30, fig. 1.

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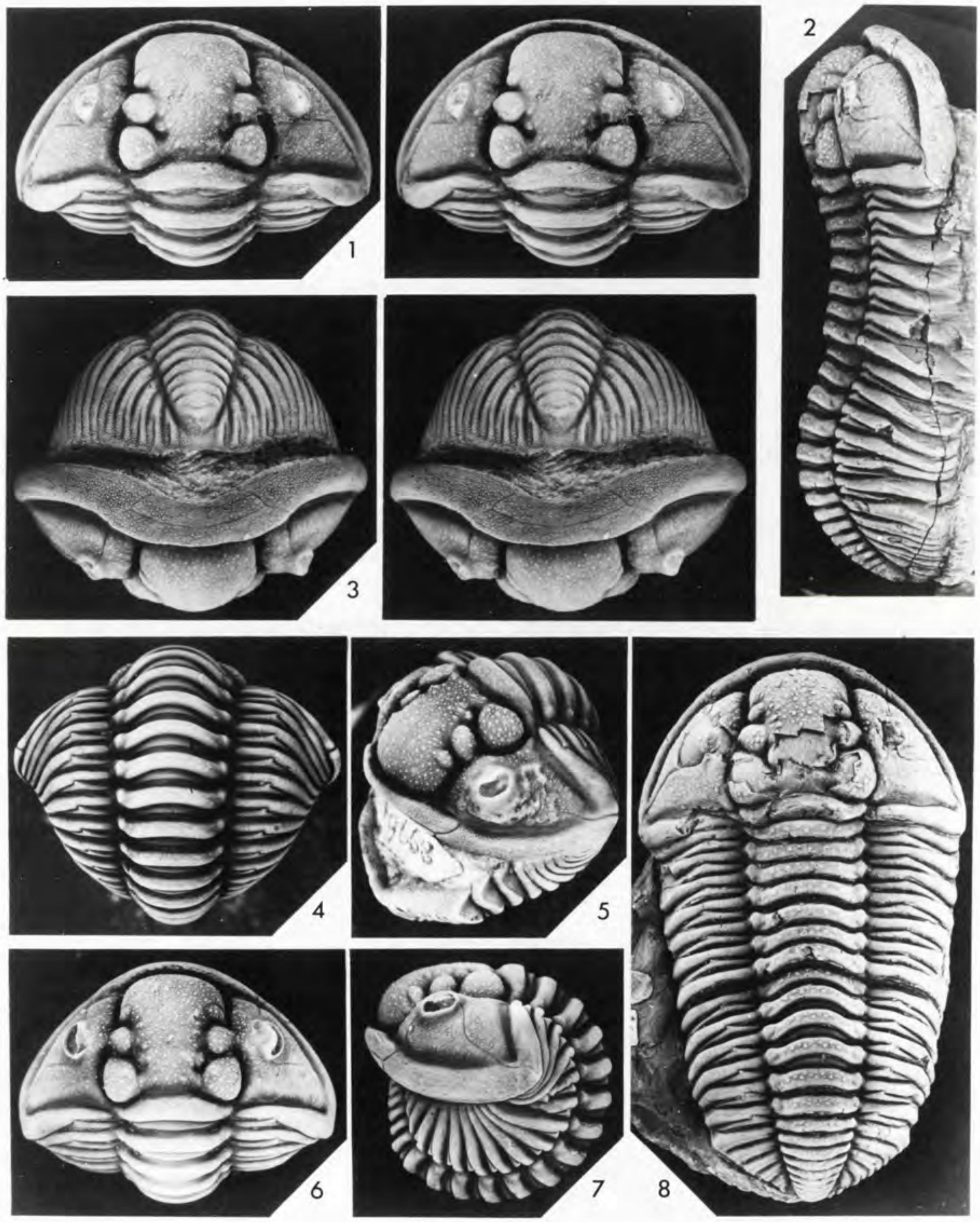

PLATE 30

Figs. 1-3. Calymene blumenbachii Brongniart, 1822

Complete, partially enrolled specimen, GSM 19668, Wenlock Limestone, Dudley. Dorsal (cephalon), frontal, dorsal (pygidium), stereo-pairs, x 2. Figured Shirley 1933, pl. 1, fig. 4, as C. blumenbachii. See also Pl. 29, figs. 4, 5.

Figs. 4-6. Calymene cf. C. neotuberculata Schrank, 1970

Incomplete cranidium, internal mould (fig. 4) and 'Silcoset' rubber cast of external mould (figs. 5, 6), GSM 103182-3, Lower Ludlow Series, scarp 80 yards S, 30 degrees W of Brynsylldy Farm, near Llanrwst, Denbighshire. Dorsal, left lateral views, x 2.

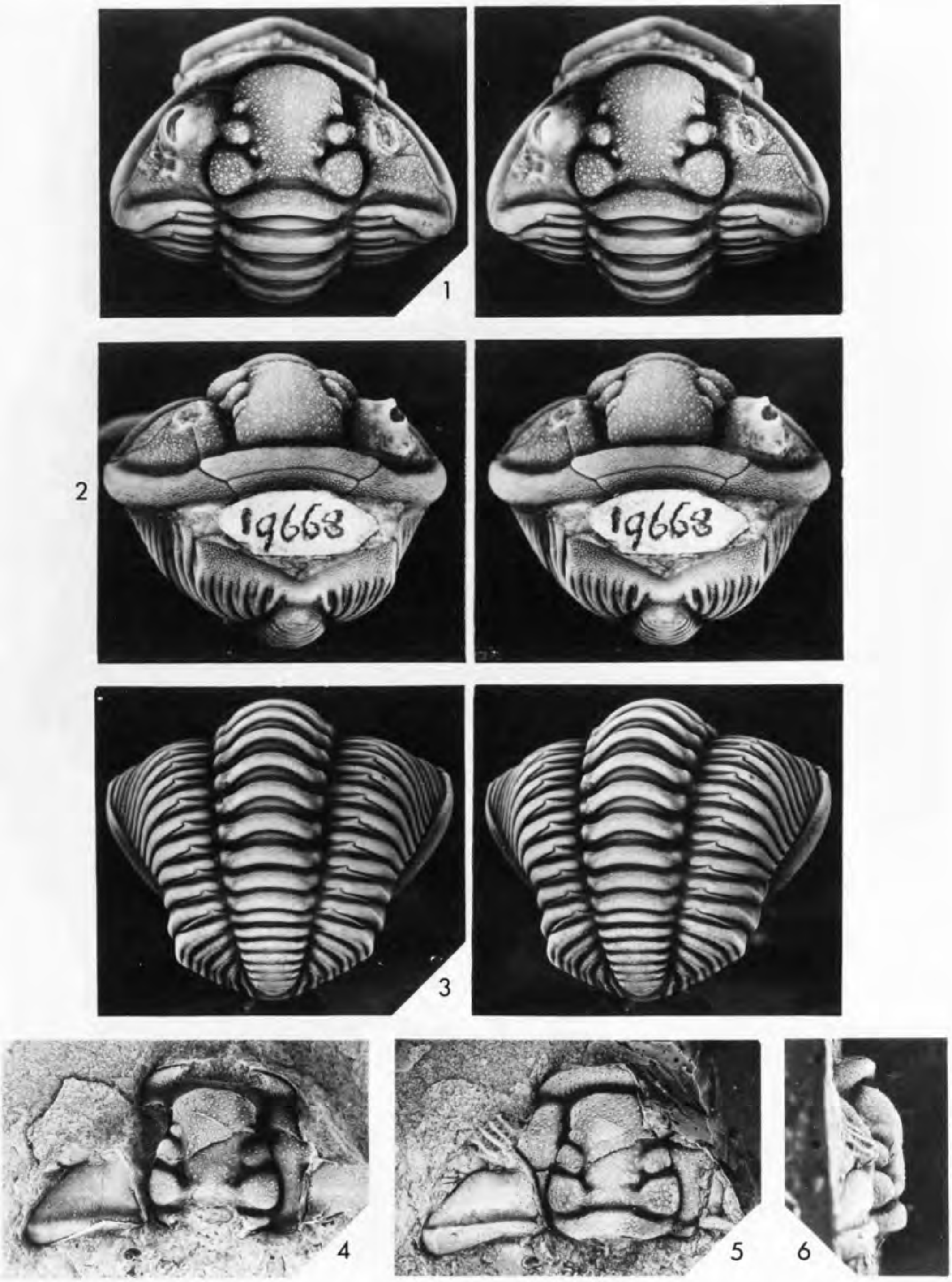
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PLATE 31

Figs. 1-9. Calymene neotuberculata Schrank, 1970

1, 3, 7. Incomplete cranidium, RM Ar27364, Mulde Beds, Djupvik, Eksta, Gotland. Dorsal stereo-pair, x 2½; left oblique stereo-pair, left lateral view, x 3.

2, 4. Incomplete cranidium, RM Ar47848, Mulde Beds, Djupvik, Eksta, Gotland. Dorsal, frontal views, x 1½.

5. Small, complete enrolled specimen, RM Ar6213, Mulde Beds, Djupvik, Eksta, Gotland. Dorsal stereo-pair, x 6.

6, 8, 9. Incomplete cranidium, RM Ar31439, Mulde Beds, Djupvik, Eksta, Gotland. Frontal, dorsal stereo-pairs, left lateral view, x 2½.

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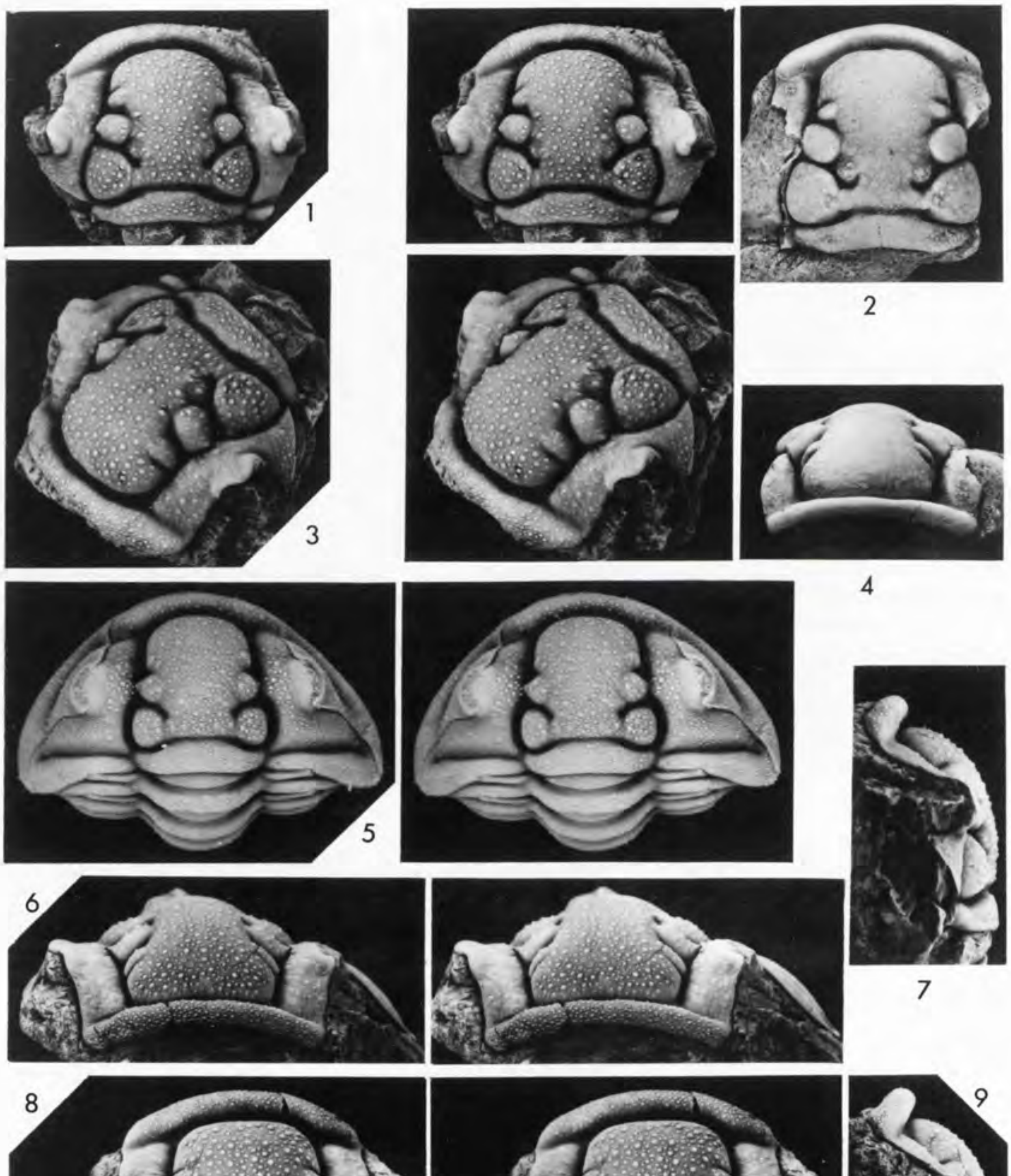

PLATE 32

Figs. 1, 2, 4-8, 10, 11. Calymene tenera Barrande, 1852

1, 2, 4, 8. Lectotype, plaster cast of incomplete cranidium, cuticle remaining on abaxial part of glabella, axial furrow and abaxial part of preglabellar area, NMP It346 CE 1252, Kopanina Formation, horizon with Cromus beaumonti (= lower Ludlovian), Jarov (Dlouha hora), Bohemia. Dorsal, left oblique stereo-pairs, frontal view, x 1½. Figured Barrande 1852, pl. 19, fig. 26.

5, 6. Paralectotype, plaster cast of pygidium, cuticle remaining on right side of axis and axial furrow, NMP It347, same horizon and locality as for fig. 1. Dorsal stereo-pair, left lateral view, x 1½. Figured Barrande 1852, pl. 19, fig. 27.

7, 10, 11. Pygidium, plaster cast of, NMP unnumbered, Kopanina Formation, Dlouha hora, Bohemia. Part of Barrande Colln. Left oblique and posterior stereo-pairs, left lateral view, x 2.

Figs. 3, 9. Calymene tenera? Barrande, 1852

Cranidium, internal mould, DJS/129, Kopanina Formation, Kosov, Bohemia. Coll. D.J. Siveter & L. Marek, 1971. Dorsal, right lateral views, x 1½.

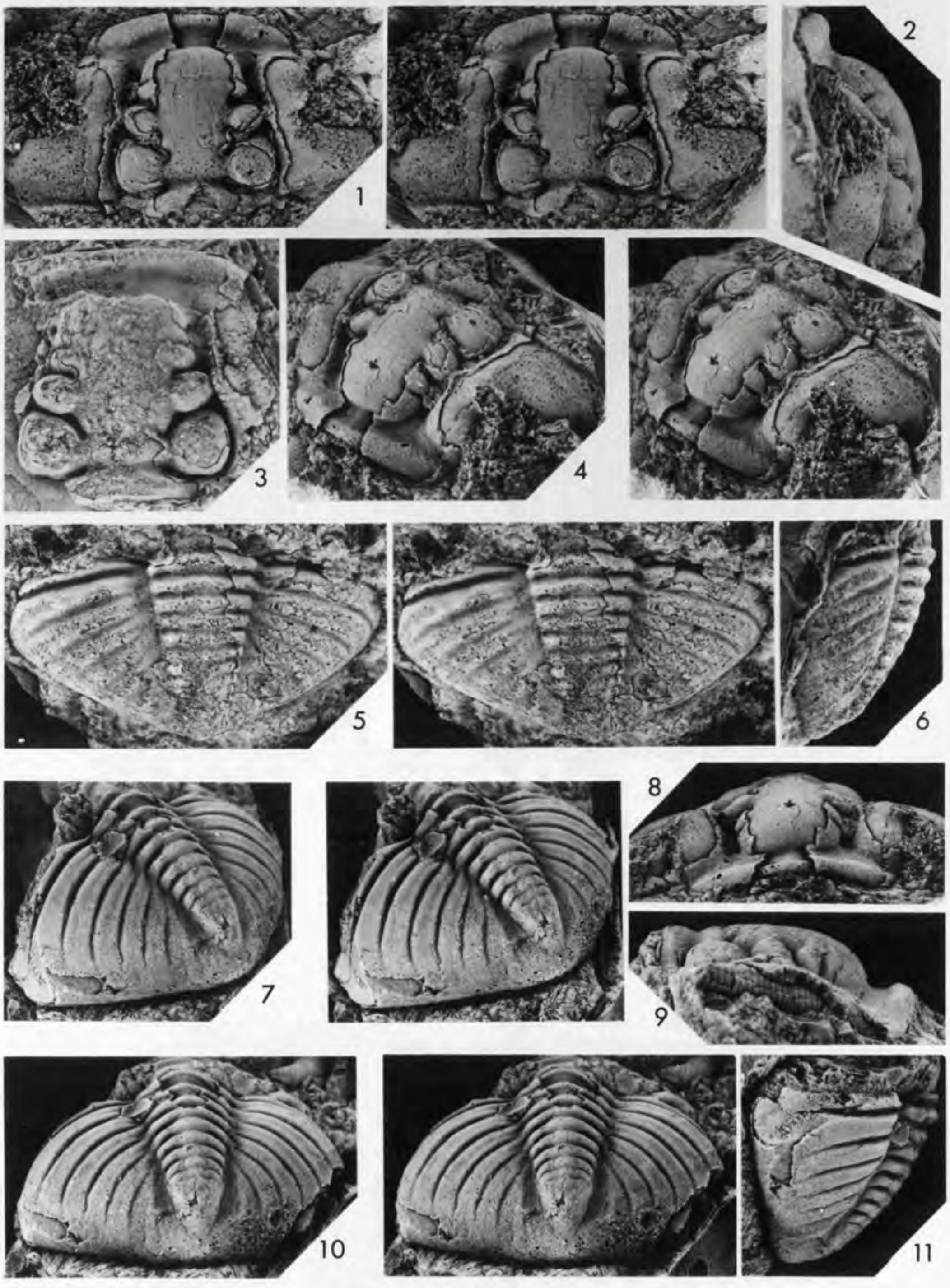
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PLATE 33

Figs. 1-8. Calymene tentaculata (Schlotheim) campana subsp. nov.

1, 2, 8. Cranidium, RM Ar32961, loose block of upper Silurian (post Whitcliffian) age, S kyrkan, loc. 4, Ramsasa, Scania. Coll. E. Stensiö, 1924. Dorsal stereo-pair, left lateral view, left oblique view, x 3½.

3-6. Holotype, cranidium, RM Ar32803, loose block of upper Silurian (post Whitcliffian) age, Ramsasa, Scania. Dorsal, frontal, right oblique stereo-pairs, right lateral view, x 2½.

7. Incomplete cranidium, RM Ar27767, Hamre or Sundre Beds, Klef i Sundre, Gotland. Dorsal stereo-pair, x 2½.

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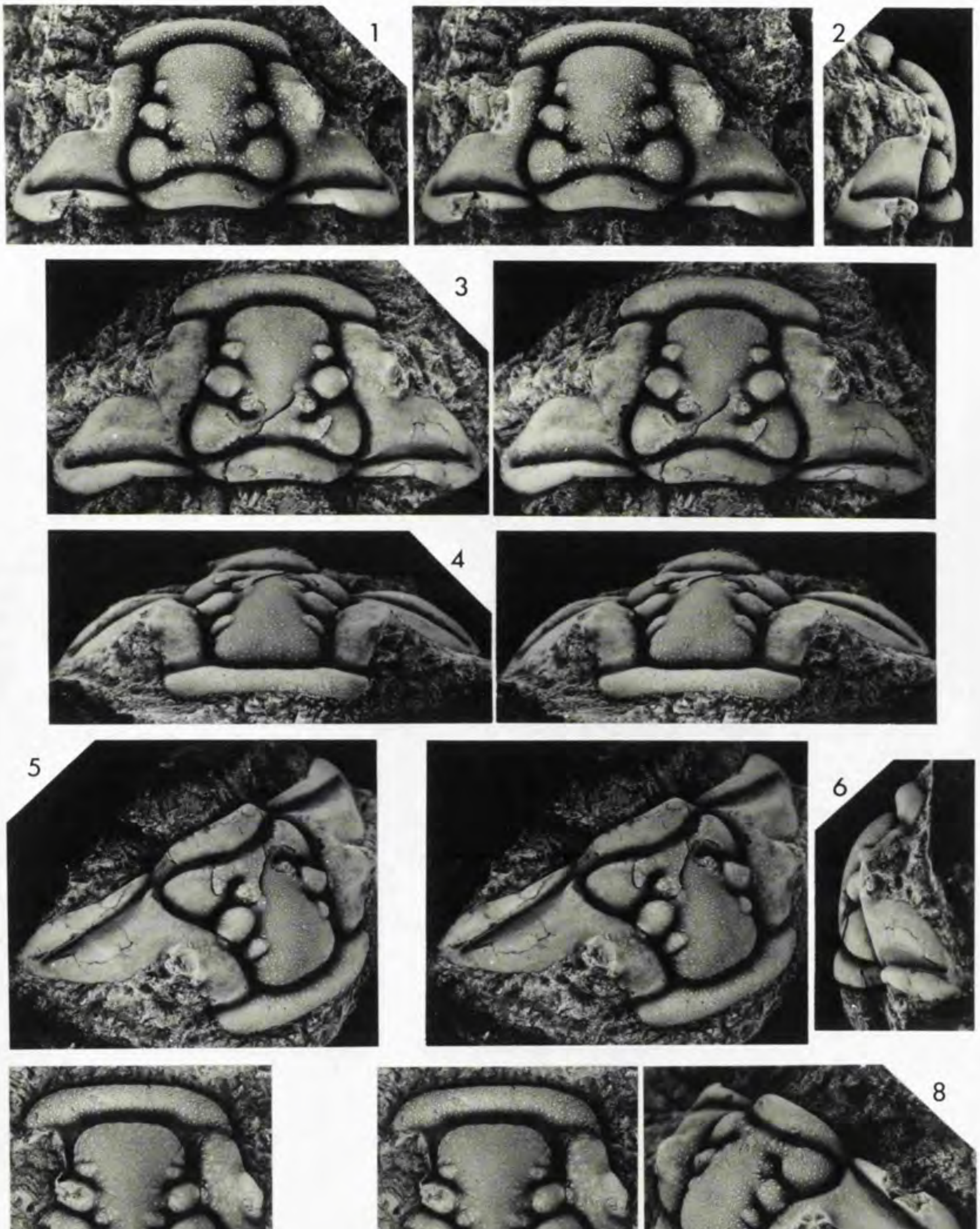

PLATE 34

Figs. 1-6. Calymene tentaculata (Schlotheim) campana subsp. nov.

1-4. Pygidium, cuticle remaining on part of left pleural region and left side of axis, RM Ar32950, loose block of upper Silurian (post Whitcliffian) age, S kyrkan, Ramsasa, Scania. Coll. E. Stensiö, 1924. Posterior stereo-pair, left lateral view, dorsal stereo-pair, left oblique view, x 1.8.

5. Cranidium, RM Ar32959, same horizon, locality and collector as for fig. 1. Dorsal view, x $2\frac{1}{2}$.

6. Pygidium, RM Ar32809, upper Silurian, Ramsasa, Scania. Posterior view, x 3.

Figs. 7-11. Calymene sp. 2

Cranidium, internal mould - GSM RK3992 (fig. 7), and 'Silcoset' rubber cast of counterpart - GSM RK3991 (figs. 8-11) lower Ludlow Series (scanicus Zone?), small disused quarry 390 yards N at 57 degrees E of Graig - bach, Denbighshire. (Nat. Grid. Ref. SH 86156225). Dorsal view (fig. 7), x $2\frac{1}{2}$; dorsal, left oblique, frontal, left lateral views, x $2\frac{1}{2}$.

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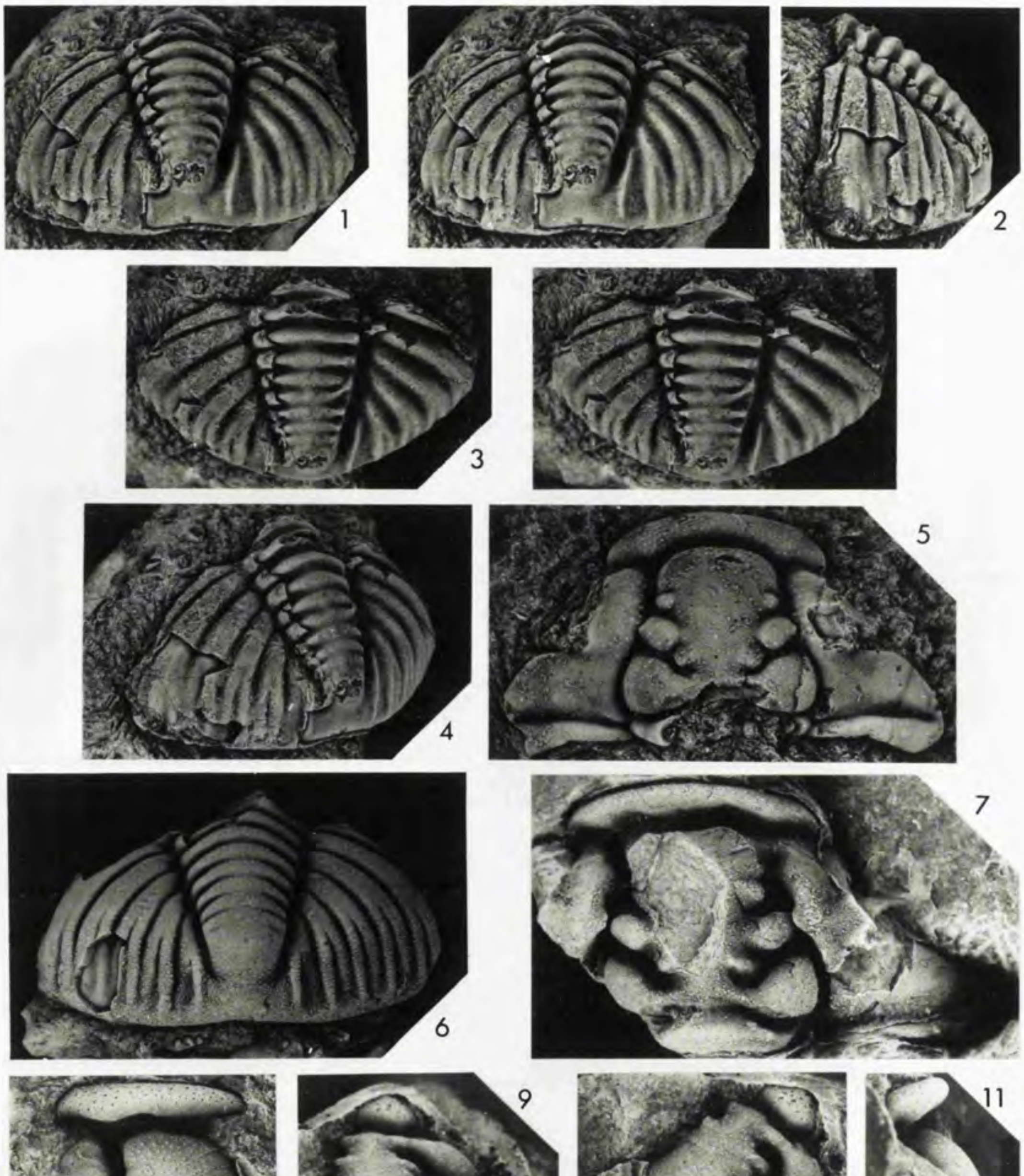

PLATE 35

Figs. 1-10. Calymene lawsoni Shirley, 1962

1-3, 7, 8. Cranidium, 'Silcoset' rubber cast of external mould (figs. 1, 3), internal mould (figs. 2, 7, 8), LE 589A, low in the Higher Lower Leintwardine Beds, Ludlow Series, Marlow lane, about $1\frac{3}{4}$ miles N of Leintwardine, Welsh Borderlands. (Nat. Grid. Ref. 4035 7679). Coll. Dr. J.H. McD. Whitaker. Dorsal stereo-pair, right oblique view, x $3\frac{1}{2}$; right lateral view, x 4; frontal view, dorsal stereo-pair, x 3.

4. Free cheek, 'Silcoset' rubber cast of external mould, LE 58/34, Higher Lower Leintwardine Beds, Ludlow Series, S side of Tatteridge Hill, about 1 mile SE of Leintwardine, Welsh Borderlands. Coll. Dr. J.H. McD. Whitaker, 'Ventral' view, x $4\frac{1}{4}$.

5. Free cheek, 'Silcoset' rubber cast of external mould, LE 289/4, Upper Leintwardine Beds, Ludlow Series, Marlow lane, about $1\frac{3}{4}$ miles N of Leintwardine, Welsh Borderlands. Coll. Dr. J.H. McD. Whitaker. 'Dorsal' view, x $4\frac{1}{4}$.

6, 10. Cranidium, internal mould, LE 289/2, base of Upper Leintwardine Beds, Ludlow Series, Marlow lane, about $1\frac{3}{4}$ miles N of Leintwardine, Welsh Borderlands. (Nat. Grid. Ref. 4086 7673). Coll. Dr. J.H. McD. Whitaker. Dorsal view, x 3; left lateral view, x 4.

9. Cranidium, internal mould, MJ 1.205a, Higher Lower Leintwardine Beds, 29 m below base of Upper Leintwardine Beds, Ludlow Series, Marlow lane, about $1\frac{3}{4}$ miles N of Leintwardine, Welsh Borderlands. Coll. Mr. M. Jones. Dorsal stereo-pair, x 5.

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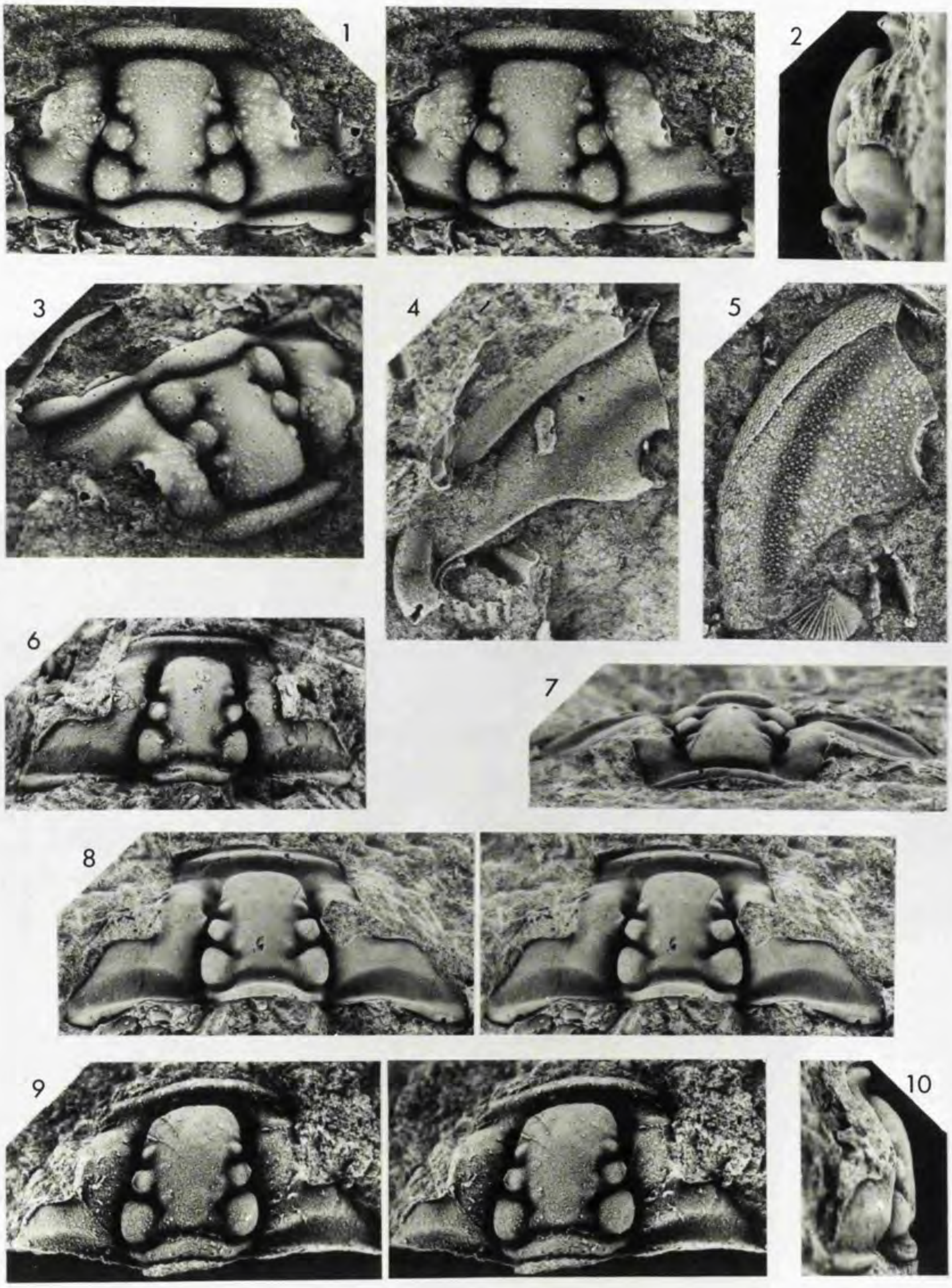

PLATE 36 (continued)

8, 10. Hypostome, 'Silcoset' rubber cast of external mould, MJ 1.194cB, Higher Lower Leintwardine Beds, 27 m from the base of Upper Leintwardine Beds, Marlow lane, about $1\frac{3}{4}$ miles N of Leintwardine, Welsh Borderlands. Coll. Mr. M. Jones. lateral view, ventral stereo- pair, x $6\frac{1}{2}$.

9. Pygidium, 'Silcoset' rubber cast of external mould, MJ 281-/2, Higher Lower Leintwardine Beds, Marlow lane, about $1\frac{3}{4}$ miles N of Leintwardine, Welsh Borderlands. Coll. Mr. M. Jones. Posterior view, x $4\frac{1}{2}$. Note pairing of pits on axis.

11. Hypostome, 'Silcoset' rubber cast of external mould, MJ P, Higher Lower Leintwardine Beds, Marlow lane, about $1\frac{3}{4}$ miles N of Leintwardine, Welsh Borderlands. Coll. Mr. M. Jones. Ventral view, x 9.

PLATE 36

Figs. 1-11. Calymene lawsoni Shirley, 1962

1. Incomplete cranidium, 'Silcoset' rubber cast of external mould, LE 289/7, base of Upper Leintwardine Beds, Ludlow Series, Marlow lane, about 1¾ miles N of Leintwardine, Welsh Borderlands. Coll. Dr. J.H. McD. Whitaker. Dorsal stereo-pair, x 10. Note pairing of large tubercles.

2-4. Incomplete cranidium, ? meraspis, internal mould (fig. 2), 'Silcoset' rubber cast of external mould (figs. 3, 4), MJ 1.132, Higher Lower Leintwardine Beds, Ludlow Series, Marlow lane, about 1¾ miles N of Leintwardine, Welsh Borderlands. Coll. Mr. M. Jones. Dorsal view, dorsal stereo-pair, right oblique view, x 11.

5. Incomplete cranidium, ? meraspis, internal mould, LE 287/5, Higher Lower Leintwardine Beds, Ludlow Series, Marlow lane, about 1¾ miles N of Leintwardine, Welsh Borderlands (Nat. Grid. Ref. 4065 7678). Coll. Dr. J.H. McD. Whitaker. Dorsal view, x 12.

6. Pygidium, 'Silcoset' rubber cast of external mould, MJ 281-/3, Higher Lower Leintwardine Beds, Ludlow Series, Marlow lane, about 1¾ miles N of Leintwardine, Welsh Borderlands. Coll. Mr. M. Jones. Posterior view, x 5. Note pairing of pits on axis.

7. Cranidium, 'Silcoset' rubber cast of external mould, LE 182/1, probably Higher Lower Leintwardine Beds, Ludlow Series, approx. ¼ mile S of Haregrove Wood, ¾ mile ENE of Leintwardine, Welsh Borderlands. Coll. Dr. J.H. McD. Whitaker. Dorsal view, x 7.

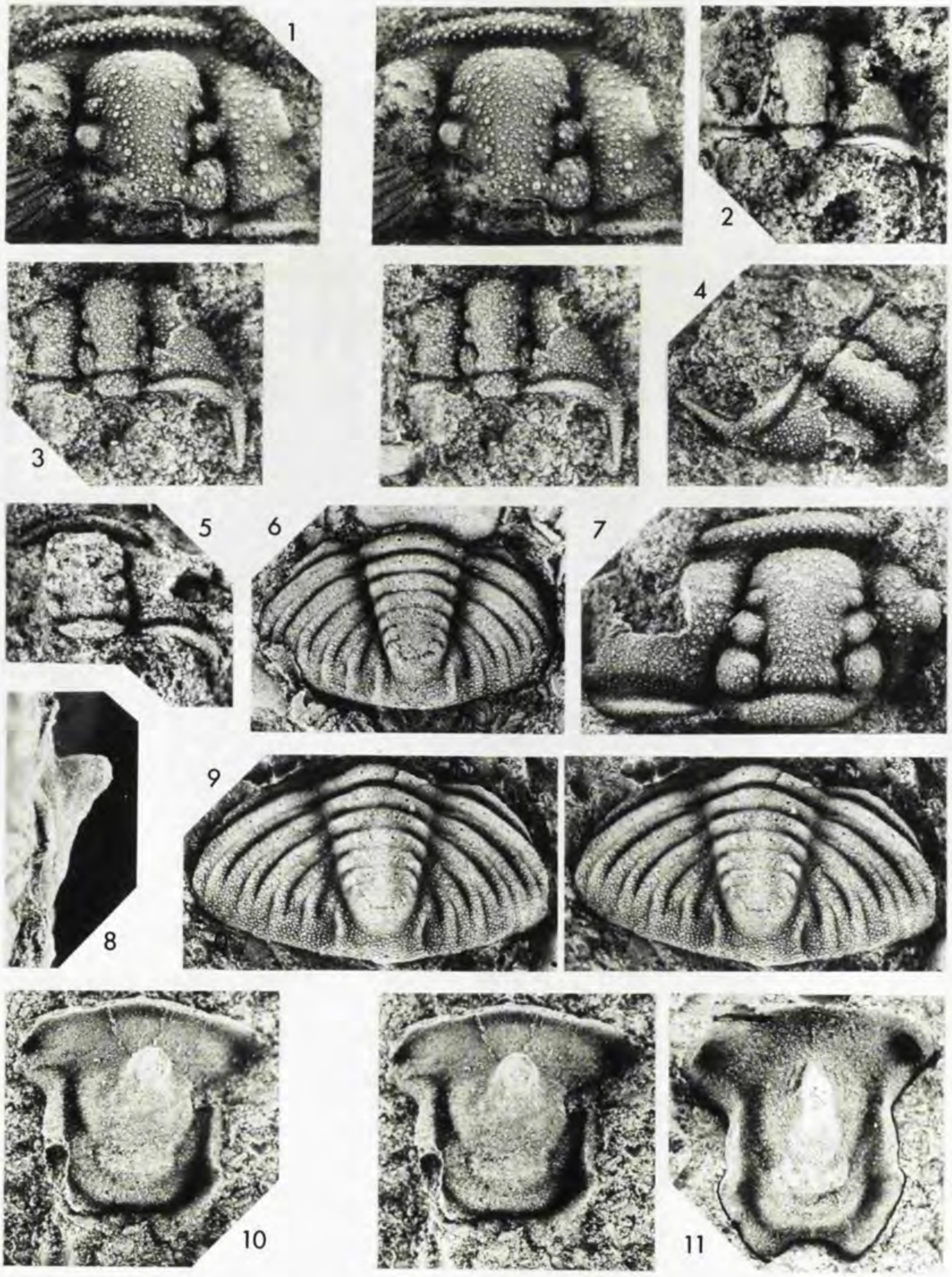
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PLATE 37

Figs. 1-5. Calymene aff. C. lawsoni Shirley, 1962

1-3. Cranidium, LM 2859, Middle Elton Beds, Upper Millichope, Wenlock Edge, Shropshire. Coll. J. Dalingwater 1965. Dorsal stereo-pair, right lateral view, frontal stereo-pair, x 3.

4. Pygidium, DJS/146, same horizon, locality and collector as for fig. 1. Posterior view, x $2\frac{1}{2}$.

5. Cranidium, DJS/145, same horizon, locality and collector as for fig. 1. Dorsal view, x 3.

Figs. 6-11. Calymene neointermedia R. & E. Richter, 1954

6. Incomplete cranidium, RM Ar47800, Hemse Beds, Petesvik, Hablingbo, Gotland. Dorsal view, x 3.

7, 10, 11. Incomplete cranidium, RM Ar47797, Hemse Beds, Petesvik, Hablingbo, Gotland. Dorsal view, right oblique stereo-pair, right lateral view, x 3.

8. Anterior part of cranidium, 'Silcoset' rubber cast of external mould, BM It9145, Wenlock Limestone, Malverns. Dorsal view, x $4\frac{1}{4}$.

9. Holotype, enrolled specimen, RM Ar6225, Hemse Beds, Petesvik, Hablingbo, Gotland. Dorsal view, x $2\frac{1}{2}$. Figured Lindström 1885, pl. 15, figs. 11, 12; Shirley 1933, pl. 1, fig. 16; Schrank 1970, pl. 1, fig. 4.

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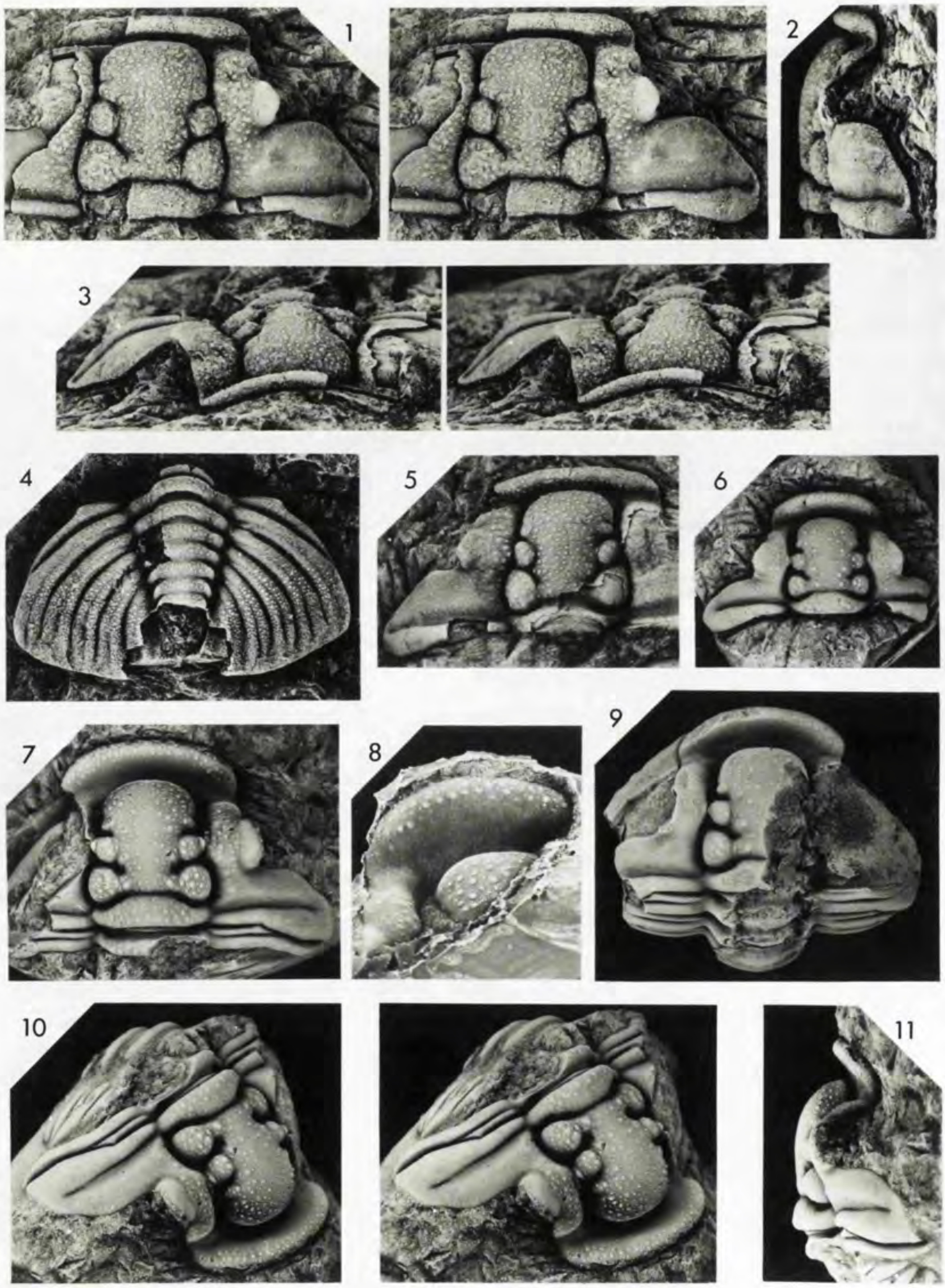

PLATE 38

Figs. 1-10. Calymene neointermedia R. & E. Richter, 1954

1, 3, Complete enrolled specimen, BM 46390 (one of five
4, 9. specimens with this number), Silurian, Gotland. Dorsal, frontal, left oblique stereo-pairs, left lateral view, x 3.

2, 6, Complete specimen, BM It9145, Wenlock Limestone, Malverns.
8, 10. Left lateral, dorsal, left oblique views, x 3; posterior view, x $6\frac{1}{4}$.

5, 7. Juvenile holaspis, damaged complete specimen, RM Ar47789, Hemse Beds, Petesvik, Hablingbo, Gotland. Dorsal view, right oblique view, x 6.

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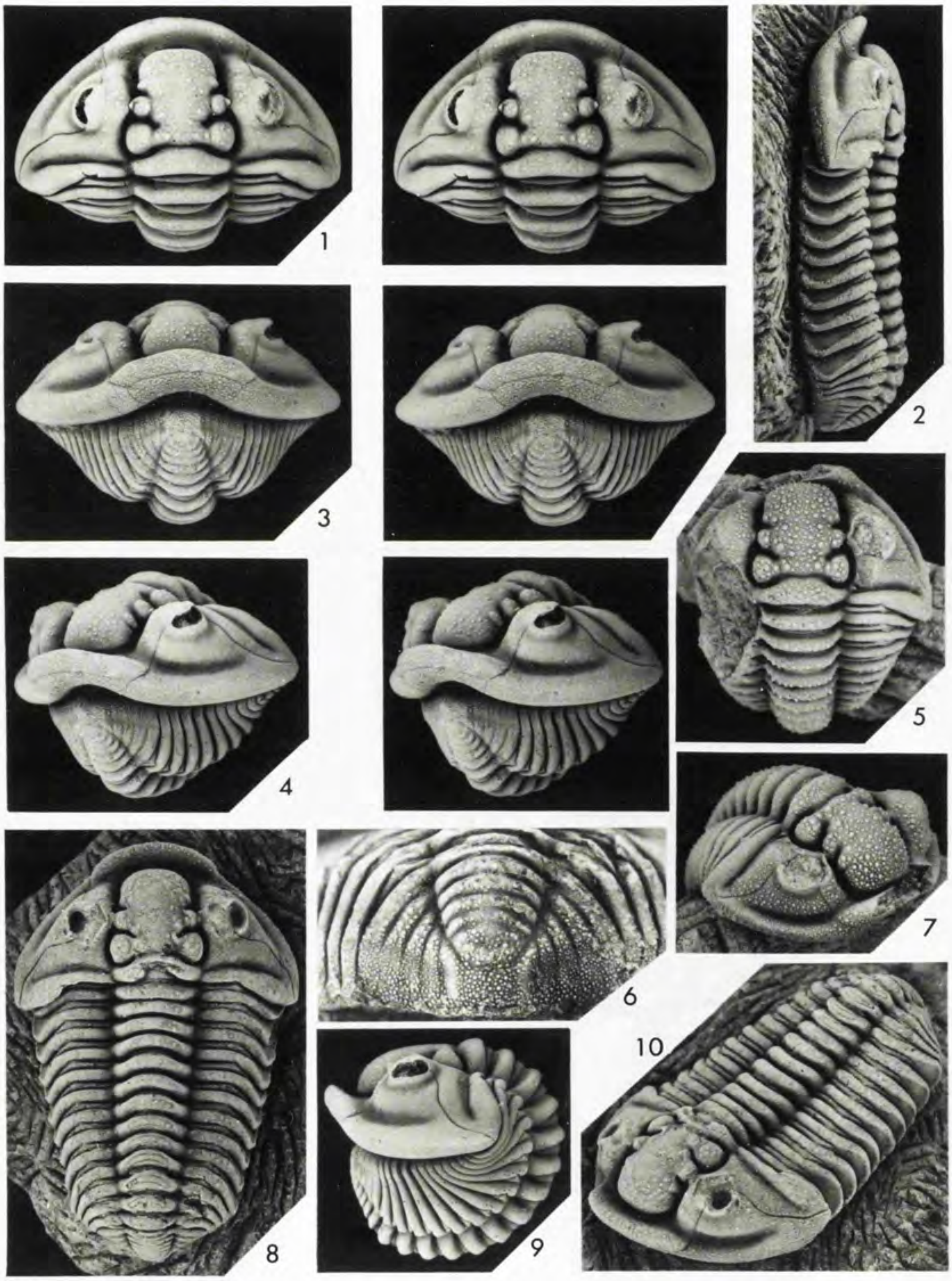

PLATE 39

Figs. 1-4, 6, 7. Calymene neointermedia R. & E. Richter, 1954

1, 3, Complete enrolled specimen, BM 43690, Silurian, Gotland.

4. Dorsal, thoracic, ventral stereo-pairs, x 2.

2, 6, Complete specimen, RM Ar47731, Silurian, Gotland.

7. Dorsal view, x 2; ventral stereo-pair of hypostome, postero-ventral view of hypostome, x 7.

Fig. 5. Calymene puellaris Reed, 1920

Damaged complete specimen, internal mould, BM It577, Upper Leintwardine Beds, lane section on the Goggin, Ludlow anticline. (Nat. Grid. Ref. SO 465695). Coll. S.F. Morris, 1963. Dorsal view, x $2\frac{1}{2}$. Note number of thoracic segments (12).

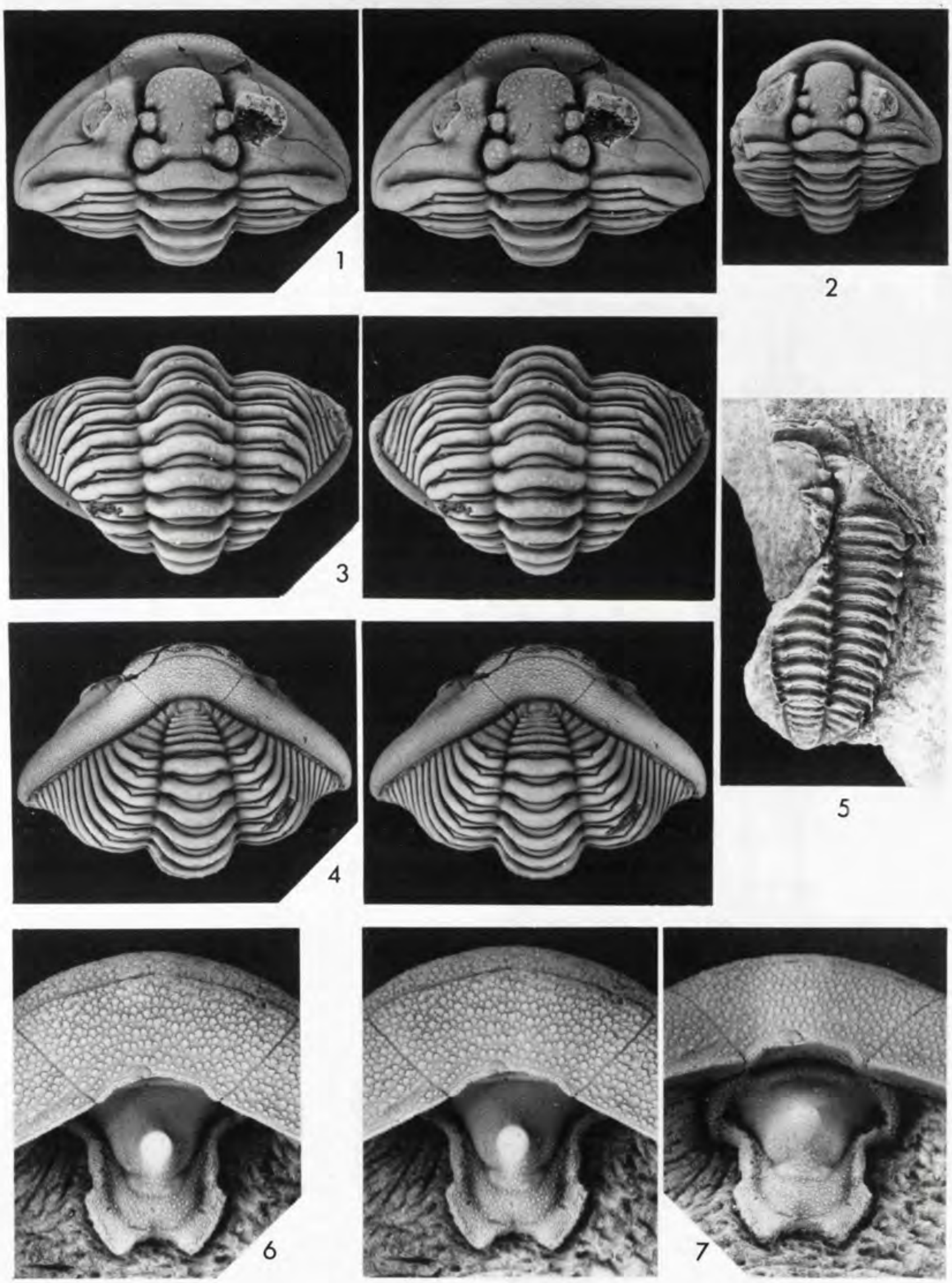
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PLATE 40

Figs. 1-7. Calymene puellaris Reed, 1920

1-3, 6. Complete specimen, RM Ar27126, Eke Beds, Eke, Alvskogs, Gotland. Dorsal, left oblique, frontal stereo-pairs, left lateral view, x 2.

4, 5, 7. Almost complete specimen, RM Ar27112, Hemse Beds, Alva Kanal, Gotland. Right lateral view, right oblique stereo-pair, dorsal view, x 3.

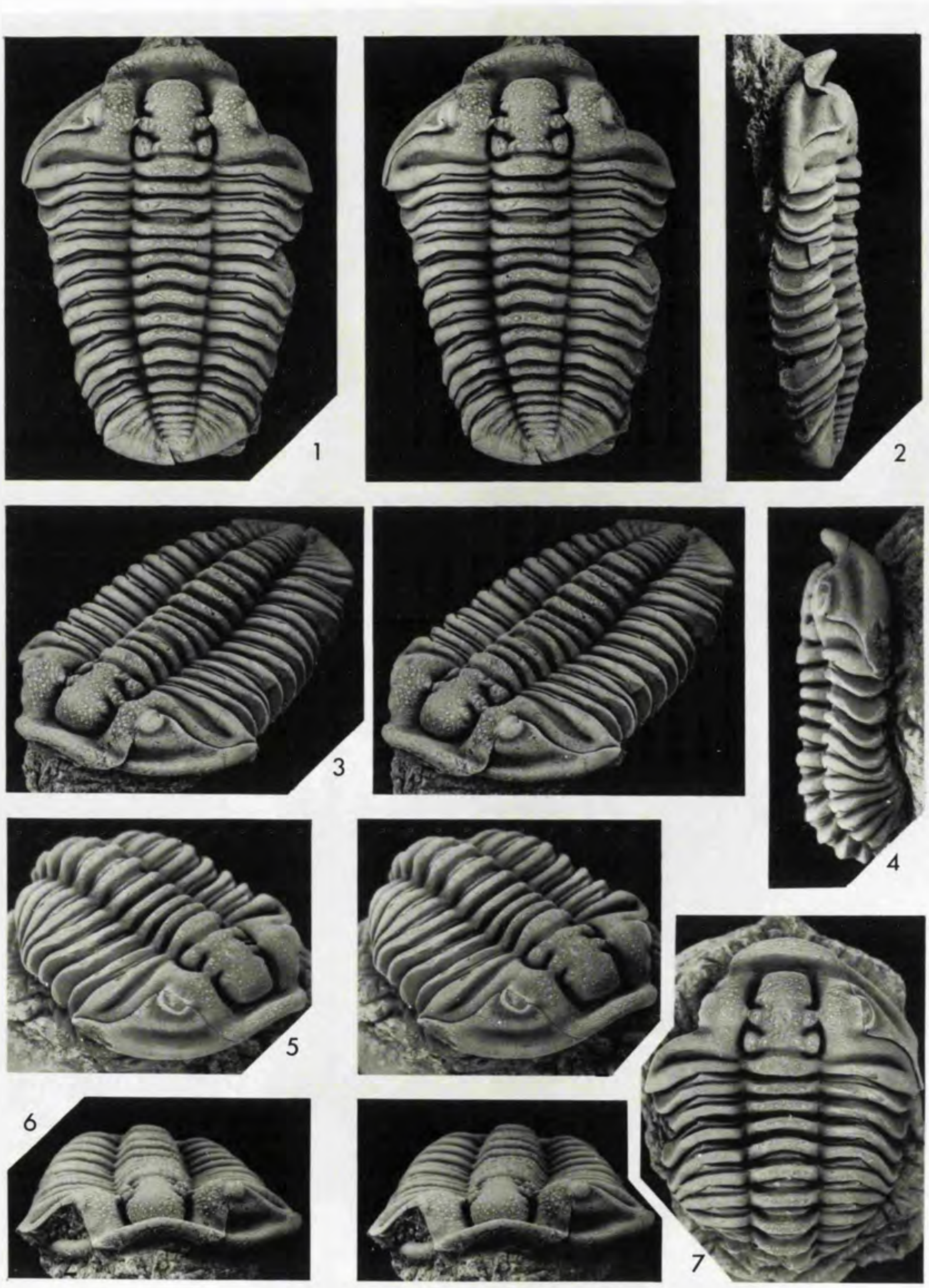
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PLATE 41 (continued)

8, 9. Cranidium, internal mould, M1, Chonetoidea (= Aegiria) grayi Beds (= Upper Leintwardinian), Builth Area, S Wales. Dorsal view, x $3\frac{1}{4}$; right oblique view, enlargement of right fixed cheek, x $7\frac{3}{4}$. Note genal spines.

PLATE 41

Figs. 1-9. Calymene puellaris Reed, 1920

1, 2, 5. Cranidium, 'Silcoset' rubber cast of external mould (figs. 1, 2), internal mould (fig. 5), DJS/132 a-b, Lower Llangibby Beds (= Upper Leintwardine in age), Ludlow Series, exposure in field by side of small stream, half a mile N of Llangibby Castle, Usk Inlier, Monmouthshire. (Nat. Grid. Ref. 368982). See Walmsley 1959, p. 495 and fig. 6. Dorsal stereo-pair, left lateral view, x 6; dorsal view, x 5.

3. Cranidium, RM Ar32767, basal Öved - Ramsasa Beds ? (see Regnell 1960, pp. 30, 31), Klinta, Scania. Dorsal stereo-pair, x 3.

4. Cranidium, 'Silcoset' rubber cast of external mould, BM It576b, Upper Leintwardine Beds, Ludlow Series, lane section on the Goggin, Ludlow anticline. (Nat. Grid. Ref. SO 465695). Coll. S.F. Morris, 1963. Dorsal stereo-pair, x 6. Note genal spine.

6. Cranidium, internal mould, SM A36815 Lower Longhope Beds?, Ludlow Series, quarry one third of a mile ENE of Longhope Church, May Hill, Gloucestershire. Locality M24 of Gardiner 1920. Topotype specimen. Dorsal view, x 2¼. Listed in Gardiner pp. 207, 218 as C. intermedia.

7. Cranidium, ? meraspis, internal mould, BM unnumbered, High Upper Leintwardine Beds, exposure on hillside 60 yards S of Halehead Farm, Corfton Bache, near Diddlebury, Wenlock Edge. Locality 214 of Shergold and Shirley Colln., Brit. Mus. (Nat. Hist.). Dorsal view, x 8. Note genal spines. Genal buttress only incipient?.

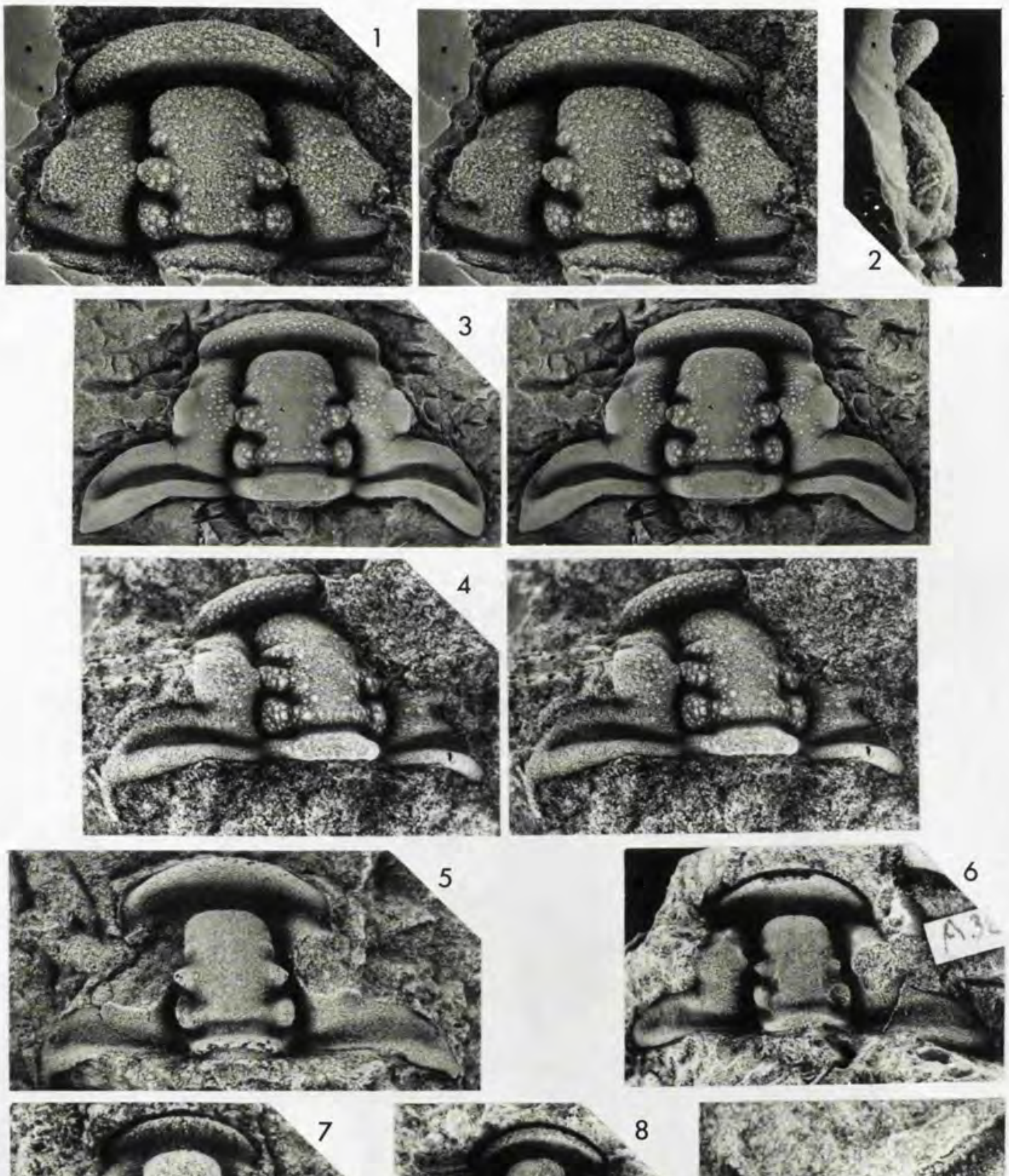
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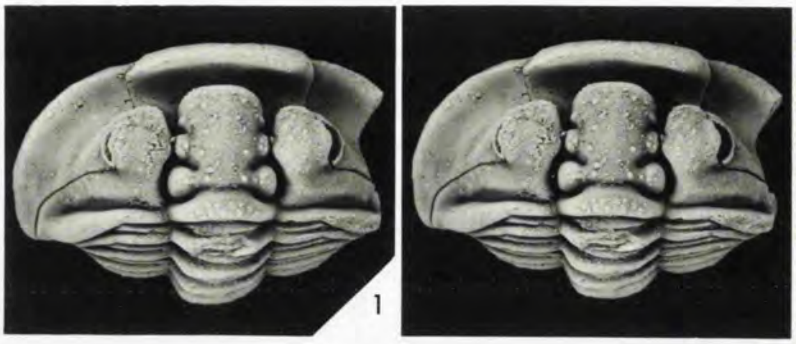
PLATE 42

Figs. 1, 3, 4, 6, 7. Calymene patustria sp. nov.

Holotype, almost complete enrolled specimen, RM Ar47855, Hemse Beds, Petesvik, Gotland. Dorsal, frontal, ventral, left oblique stereo-pairs, left lateral view, x 3.

Figs. 2, 5. Calymene puellaris Reed, 1920

Holotype, damaged complete specimen, internal mould, SM A3320, Lower Longhope Beds ?, Ludlow Series, quarry one third of a mile ENE of Longhope Church, May Hill, Gloucestershire. Locality M24 of Gardiner 1920. Dorsal view, posterior oblique view, x 2½. Figured F.R.C. Reed in Gardiner 1920, p. 221 as C. puellaris; also Shirley 1933, p. 63, pl. 1, fig. 15 as C. cf. intermedia Lindström. Note number of thoracic segments (12).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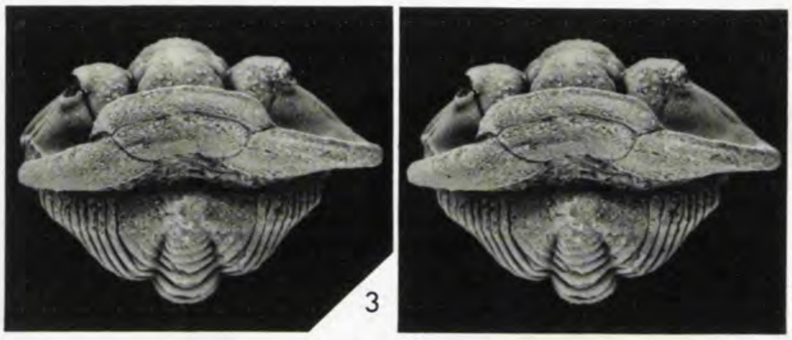
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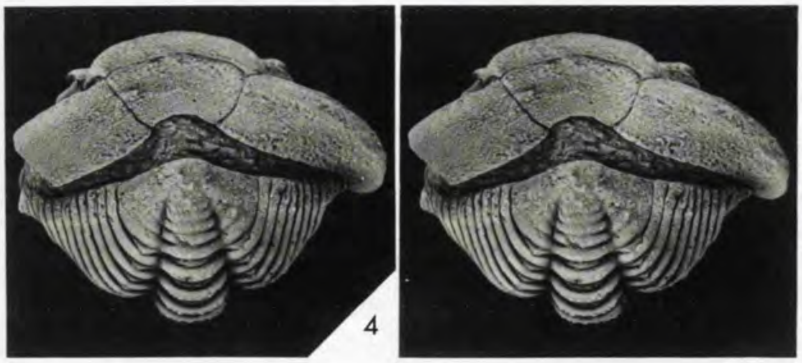
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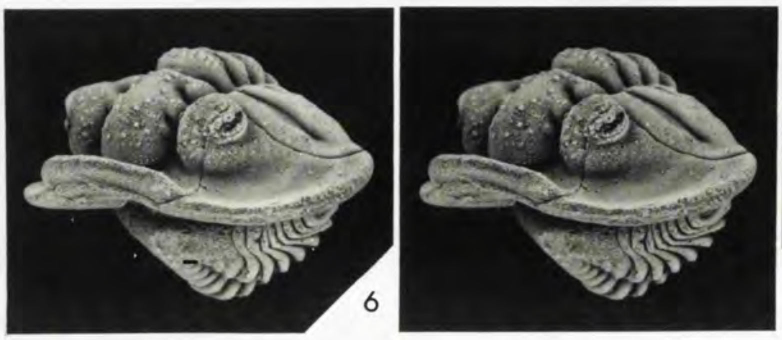
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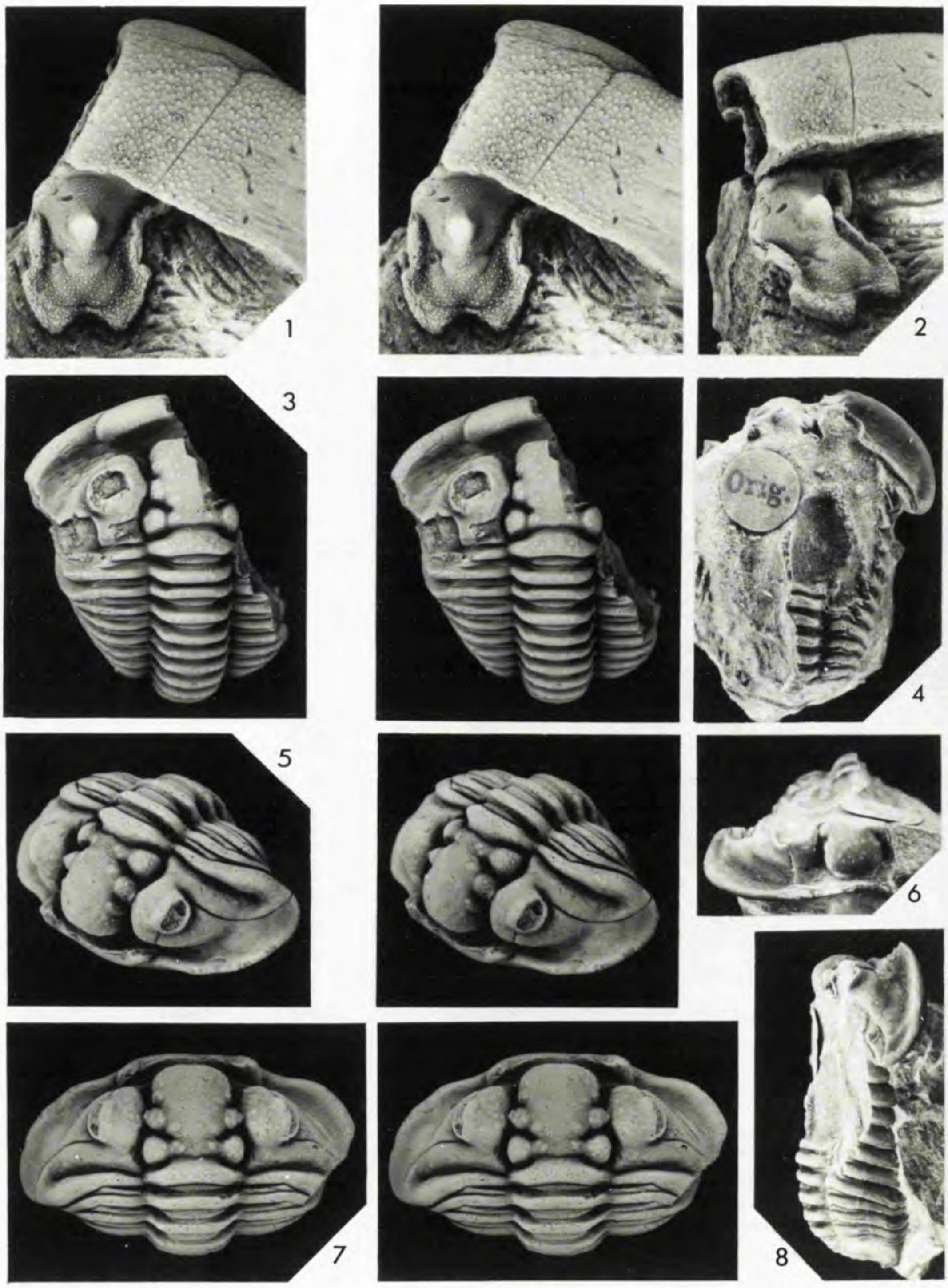
PLATE 43

Figs. 1-8 . Calymene patustria sp. nov.

1-3. Damaged complete specimen, RM Ar27151, Hemse Beds, Petesvik, Hablingbo, Gotland. Ventral stereo-pair of hypostome, oblique view of hypostome, x 7; dorsal stereo-pair, x 3.

4, 6, 8. Very badly damaged complete specimen, RM Ar6222, Hemse Beds, Petesvik, Hablingbo, Gotland. Dorsal, frontal, left lateral views, x 2. Figured Lindström 1885, pl. 15, fig.5 as C. intermedia Lindström.

5, 7. Damaged complete enrolled specimen, RM Ar27150, Hemse Beds, Petesvik, Hablingbo, Gotland. Left oblique, dorsal stereo-pairs, x 3.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CHAPTER F PLATES 1-8

PROBOSCIDEAN TRENDS IN CALYMENID TRILOBITES FROM THE ORDOVICIAN AND SILURIAN OF NW EUROPE, THE UNITED STATES AND SE ASIA.

PLATE 1

Figs. 1-10. Tapinocalymene volsoriforma sp. nov.

1-4. Holotype, incomplete cranidium, GSM Zs63, Garwood Coll., probably from the shale band near the base of the Dolyhir limestone, lowest Wenlock Series, Dolyhir, Radnorshire. See discussion of type stratum and type area. Dorsal, frontal, left oblique stereo-pairs, x 2.25; right lateral view, x 3.

5, 10. Incomplete cranidium and left free cheek, GSM Zs65, Garwood Coll., same stratum and area as holotype. Left oblique and dorsal views, x 2.

6-8. Almost complete cephalon and rostral plate, GSM Zs58, Garwood Coll., same stratum and area as holotype. Dorsal, left oblique, ventral views, x 2. See also Pl. 2, fig. 10.

9. Incomplete pygidium, exoskeleton removed from outer part of pleural region, GSM Zs64, Garwood Coll., same stratum and area as holotype. Dorsal view, x 2.25.

1

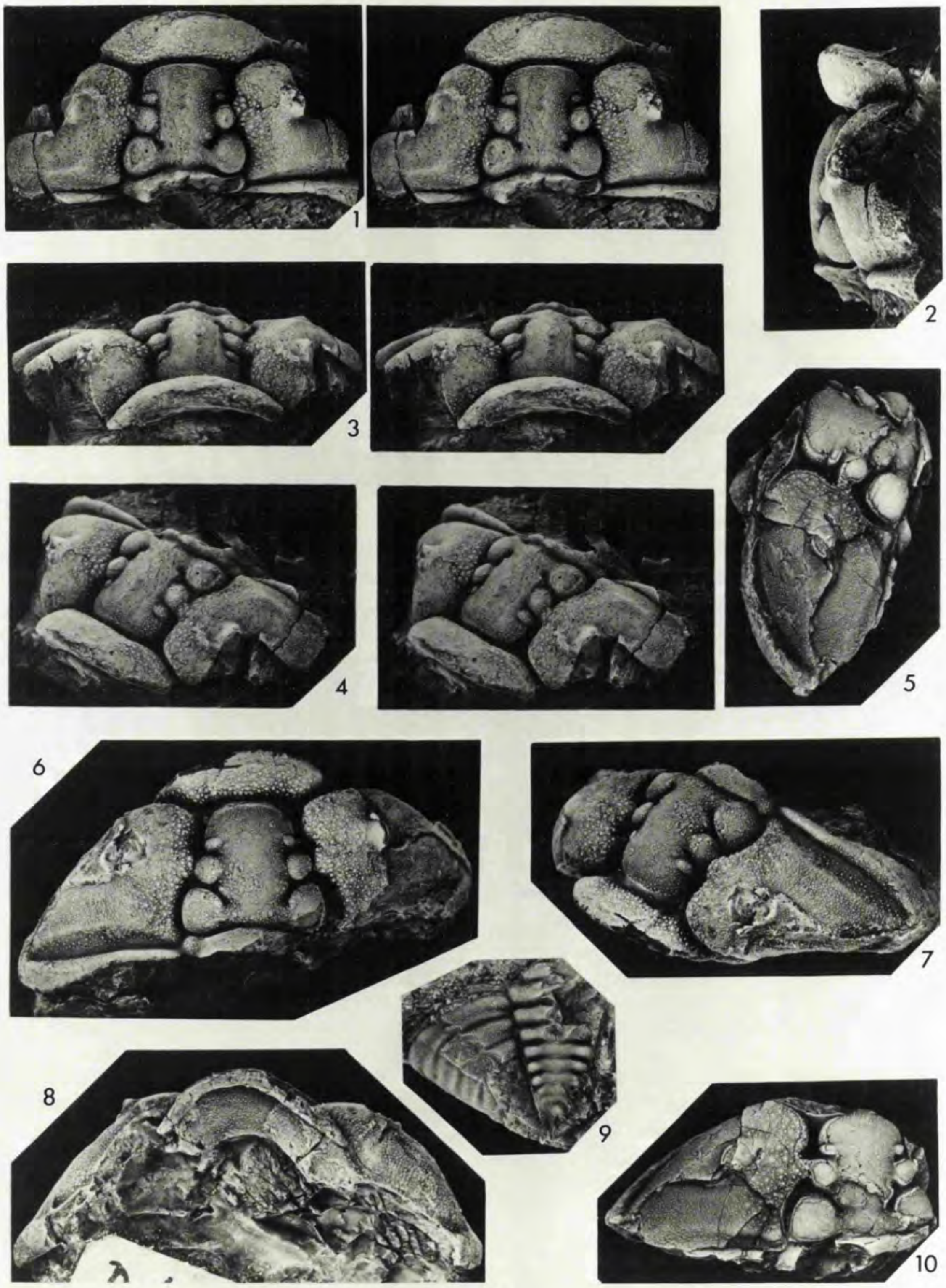


PLATE 2

Figs. 1-7, 9, 10. Tapinocalymene volsoriforma sp. nov.

1, 3. Incomplete cranidium, LM 2850 a-b, specimen found in a water-transported pebble, near English bridge, Shrewsbury. Coll. K. Walters. 'Silcoset' cast of external mould, LM 2850b, dorsal stereo-pair, x 2.25; internal mould, LM 2850a, dorsal view, x 2.25.

2, 7. Incomplete pygidium, GSM Zs61, Garwood Coll., same stratum and area as holotype. Left lateral and dorsal views, x 2.25.

4, 5, 9. Incomplete cranidium, GSM Zl 9983, Garwood Coll., same stratum and area as holotype. Dorsal, left lateral, left oblique views x 2.

6. Incomplete hypostome, GSM Zl 9696, Garwood Coll., same stratum and area as holotype. Ventral stereo-pair, x 5.

10. Glabella, GSM Zs58, Garwood Coll., same stratum and area as holotype. Enlargement of Pl. 1, fig. 6, x 4. See also Pl. 1, figs. 7, 8.

Figs. 8, 11. Tapinocalymene cf. T. volsoriforma sp. nov.

'Silcoset' cast of external mould of incomplete cephalon, DJS/89b Wenlock Shale, road cutting on the north side of a bend in the A489 road between Horderley and Plowden, S side of Long Mynd, Shropshire. Coll. Mr. C.N. Rodgers. Enlargement of left fixed cheek and part of glabella, dorsal view, x 4; dorsal view, x 2.

2

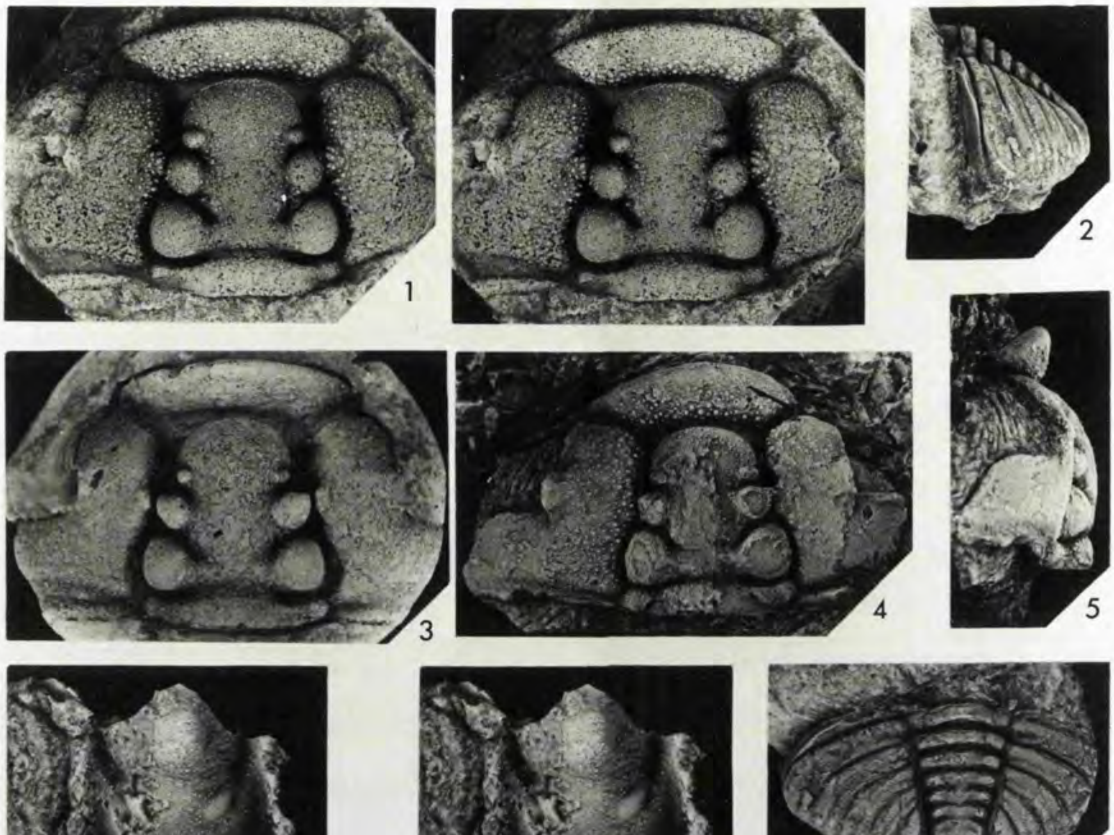


PLATE 3

Figs. 1-12. *Tapinocalymene vulpecula* sp. nov.

1, 2, 12. Holotype, incomplete cranidium, DJS/48, Wenlock Shale, small old quarry on the western side of the road from Letton to Walford, quarter of a mile north of Letton, near Wigmore Rolls area, Welsh Borderland. Nat. Grid Ref. SO 70803790. Coll. Derek J. Siveter, 1971. Dorsal stereo-pair, left lateral, left oblique views, x 2.5.

3, 11. 'Silcoset' cast of external mould of hypostome, DJS/78b, topotype specimen. Coll. Derek J. Siveter, 1971. Dorsal stereo-pair, left lateral view, x 10.

4. Internal mould of a pygidium, DJS/80, topotype specimen. Coll. Derek J. Siveter, 1971. Dorsal view, x 2.5.

5. Incomplete pygidium, DJS/79, topotype specimen. Coll. Derek J. Siveter, 1971. Dorsal view, x 2.5.

6, 8, 10. Incomplete cranidium, DJS/77, topotype specimen. Coll. Derek J. Siveter, 1971. Right oblique, dorsal, frontal views, x 4.

7. Incomplete cranidium, DJS/75, topotype specimen. Coll. Derek J. Siveter, 1971. Dorsal view, x 2.5.

9. Incomplete cranidium, DJS/76, topotype specimen. Coll. Derek J. Siveter, 1971. Dorsal view, x 2.5.

3

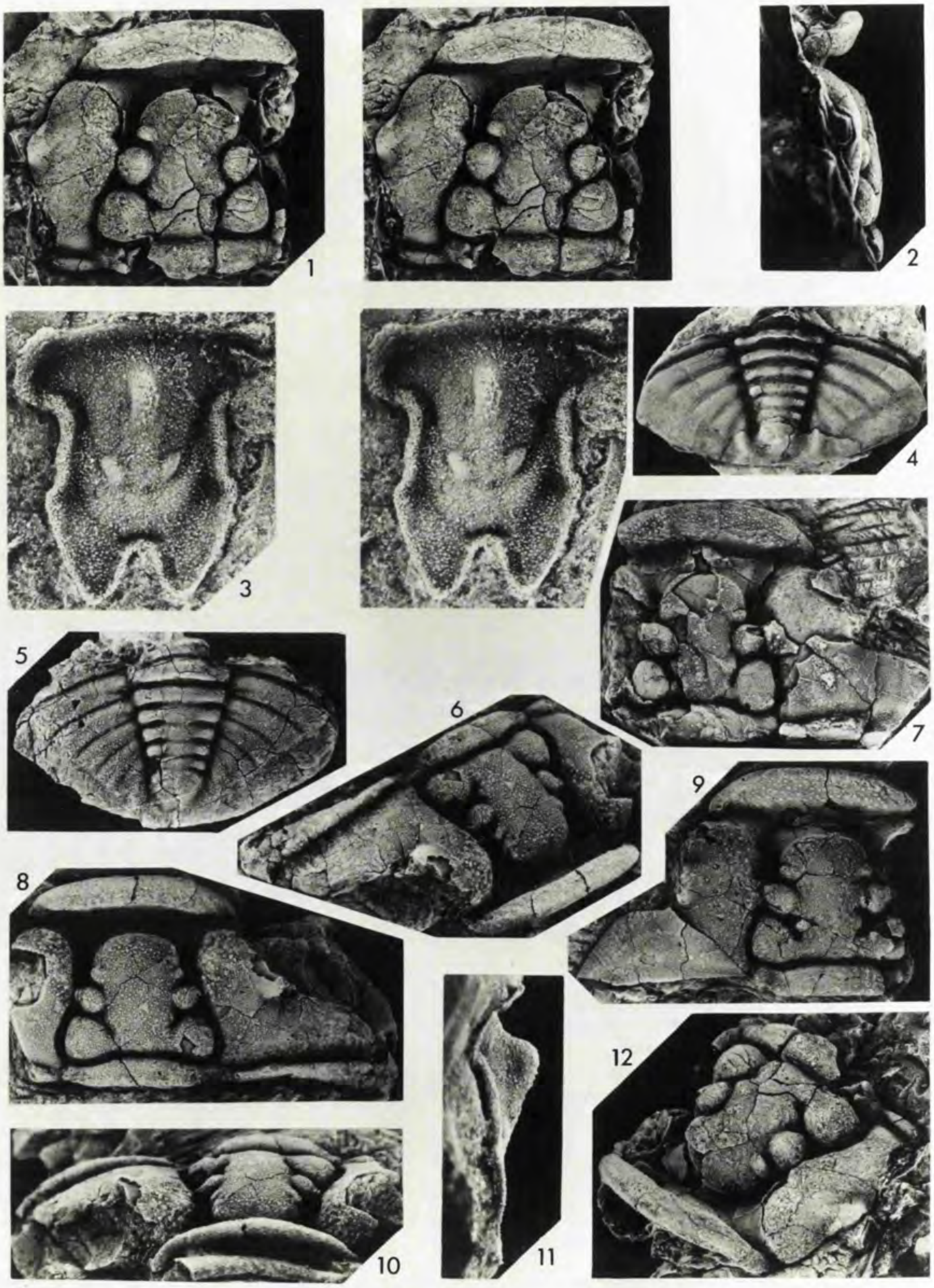


PLATE 4

Figs. 1-7. Tapinocalymene nodulosa (Shirley, 1933)

1, 3, 5, 6. Almost complete enrolled individual, lacking free cheeks, HM A212/1, Wenlock Shale, Burrington, Herefordshire. Dorsal, frontal, left oblique stereo-pairs, x 1.75; left lateral view, x 2.

2, 4. Twelve thoracic segments and attached pygidium, RMO 1300, Wenlock Shale, Burrington, Herefordshire. Coll. Dr. R.M. Owens. Dorsal view of left part of thoracic axis and adaxial part of pleural region, left lateral view of twelve thoracic segments, showing kink in posterior margin of posterior pleurae becoming successively lower on anterior pleurae, x 3.2. See also Pl. 5, figs. 4-6.

7. Cranidium, DJS/49, Wenlock Shale, C. lundgreni Zone, main sunken road, Burrington, Herefordshire. Nat. Grid Ref. SO 44237184. Coll. Derek J. Siveter, 1971. Dorsal view, x 2. See also Pl. 5, fig. 8.

4

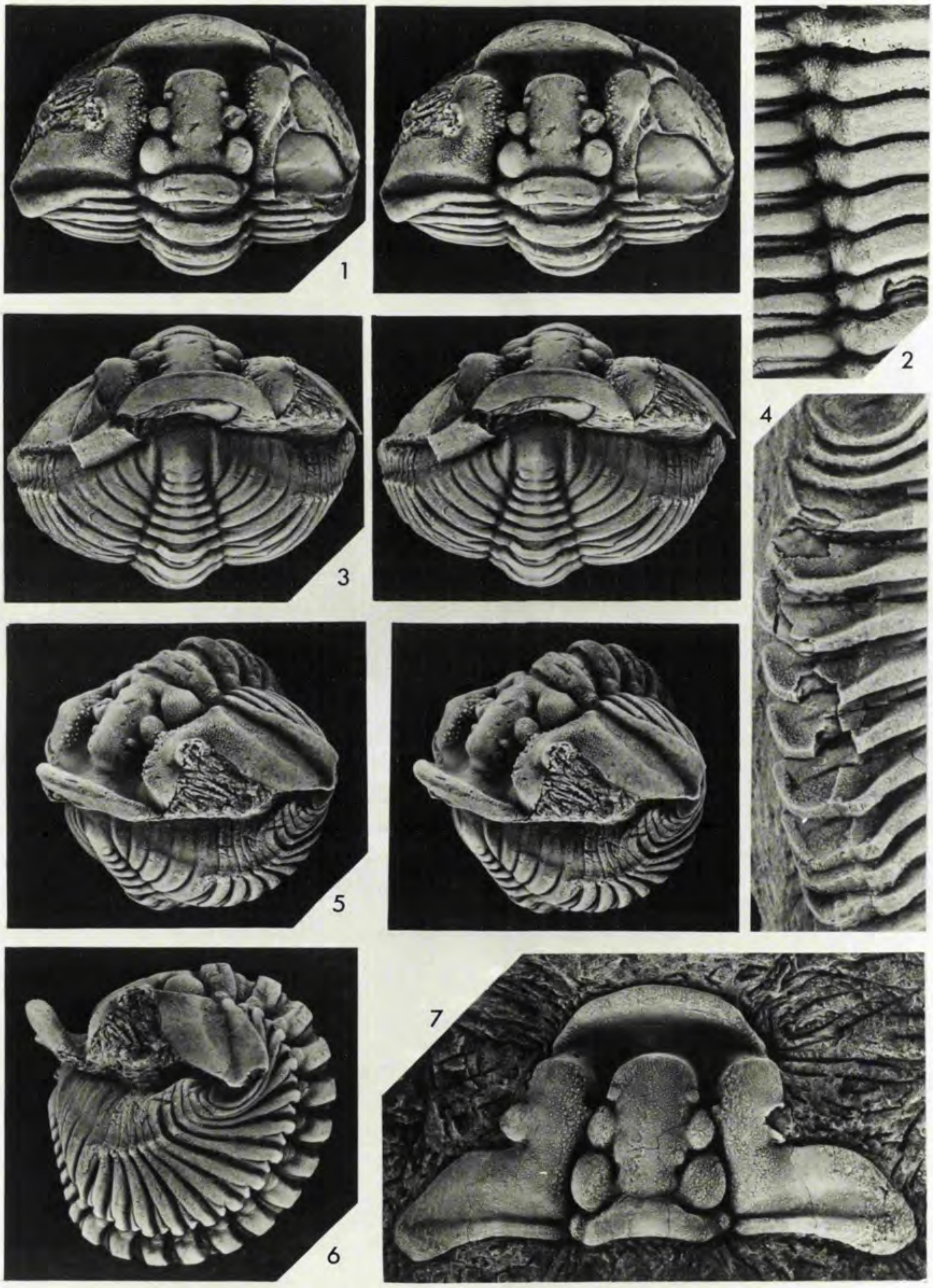


PLATE 5 (continued)

8. Cranidium, DJS/49, Wenlock Shale, sunken road, Burrington, Herefordshire. Coll. Derek J. Siveter, 1971. Left oblique view, x 2. See also Pl. 4, fig. 7.

PLATE 5.

Figs. 1-10. Tapinocalymene nodulosa (Shirley, 1933)

1-3. Holotype, almost complete individual lacking preglabellar area, cuticle removed from abaxial part of thorax and cephalon, GSM 19642, Wenlock Shale, Burrington, Herefordshire. Dorsal stereo-pair of thorax and pygidium, left lateral view, x 1.5; dorsal view of cephalon, x 2. Original of Shirley, 1933, pl. 1, figs. 6-10.

4-6. Pygidium and twelve attached thoracic segments, RMO 1300, Wenlock Shale, Burrington, Herefordshire. Coll. Dr. R.M. Owens. Dorsal, left lateral, posterior views, x 1.5. See also Pl. 4, figs. 2, 4.

7, 9, 10. Pygidium, NMW 53.288.G.1. This specimen is labelled as coming from the "Woolhope Limestone, Dolyhir quarry, two and a half miles S E of New Radnor, Radnorshire". However the lithology of its surrounding matrix is very different to that of the Dolyhir (lateral equivalent of the Woolhope) Limestone; it is enclosed in a calcareous nodule identical to those found within the small, faulted patch of Wenlock Shale in Dolyhir new quarry (see Garwood & Goodyear 1918, p.20). Calcareous nodules or concretions containing the same species have been collected from the Wenlock Shale of this quarry by the present author, and are also present in the coll. of the Geol. Surv. Mus. (see Pl. 6, figs. 1, 4, 6, 7, 10, 11) and Brit. Mus. (In 36405-6, It 2396). The age of this specimen is thus regarded as Wenlock Shale. Donor, T. Evans. Posterior, right lateral views, x 1.5; right oblique view, x 2.

5

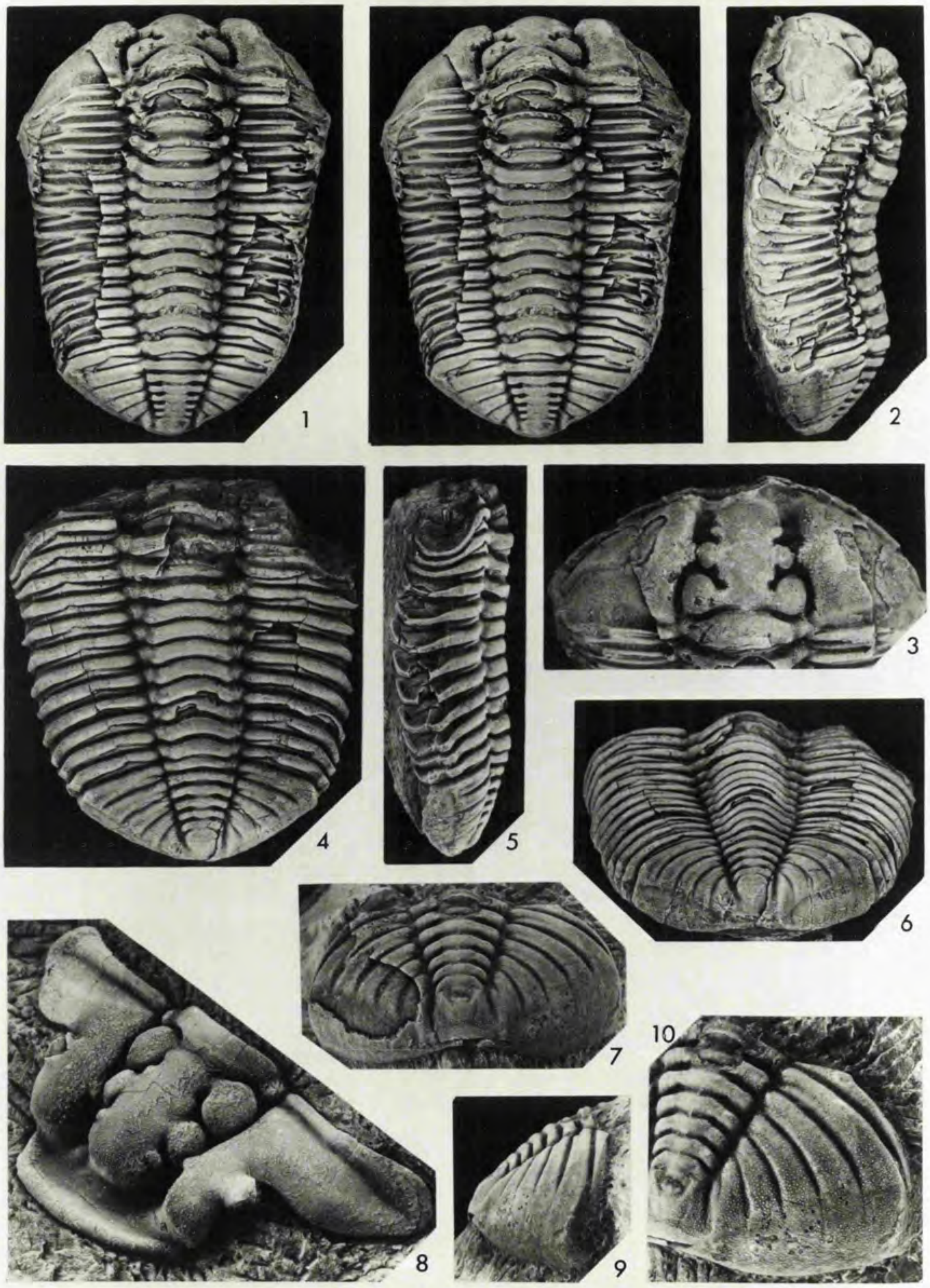


PLATE 6.

Figs. 1-12. Tapinocalymene nodulosa (Shirley, 1933)

1, 4, 7. Incomplete cranidium lacking abaxial part of right fixed cheek, GSM Zs195, Garwood Coll., enclosed in calcareous nodule, Wenlock Shale, Dolyhir, Radnorshire. This specimen probably comes from the faulted area of Wenlock Shale, on top of the Dolyhir Limestone, Dolyhir new quarry. See Garwood & Goodyear 1918, p. 20. Dorsal, left oblique views x 2; right lateral view, x 3.

2, 3. Incomplete cranidium lacking preglabellar area, LM 4902, Wenlock Shale, Burrington, Herefordshire. Dorsal view, whole specimen, x 0.7; dorsal view, enlargement of glabella, note pattern of tubercles and strong trace of eye ridge in axial furrow, x 4.

5, 8. Incomplete cranidium, LM 4885, Wenlock Shale, lundgreni Zone, sunken road, Burrington, Herefordshire. Nat. Grid Ref. SO 4423 7184. Coll. H. Baker & W.J. Norton, 1968. Dorsal and front views, x 2.

6, 10, 11. Incomplete cranidium, GSM Zs183, Garwood Coll., Wenlock Shale, Dolyhir, Radnorshire. Exact locality probably the same as GSM Zs195, Pl. 6, figs. 1, 4, 7. Dorsal, right oblique views, x 2; right lateral view, x 3. See also Pl. 7, fig. 4.

9, 12. Pygidium, DJS/51, Wenlock Shale, lundgreni Zone, main sunken road, Burrington, Herefordshire. Coll. Derek J. Siveter, 1971. Dorsal and posterior views, x 6.

6

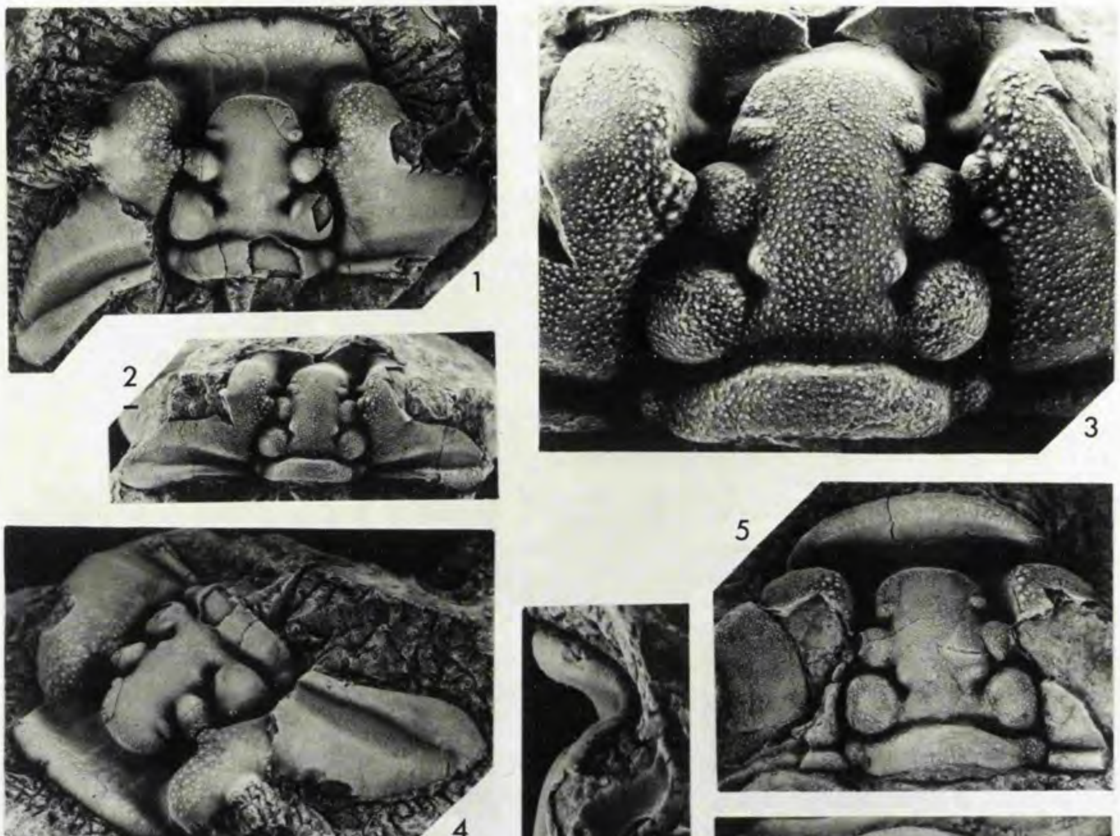


PLATE 7

Figs. 1-9. Tapinocalymene nodulosa (Shirley, 1933)

1, 3. Outer side of anterior border, rostral plate and hypostome, RM Ar38841, Wenlock Shale, Burrington, Herefordshire. Ventral and postero-ventral stereo-pairs, x 3.5. Note hooked projection and conspicuous maculae of hypostome.

2, 7, 8. Incomplete cranidium and its rostral plate, DJS/3a, Wenlock Shale, lundgreni Zone, sunken road, Burrington, Herefordshire. Coll. Derek J. Siveter, 1971. Ventral view of axial furrow showing pit on ventrally projecting boss for reception of anterior process of hypostome, and forked ridge posterior to boss, x 8; rostral plate and outer part of anterior border, ventral view, x 4; ventral stereo-pair of cranidium, x 2.

4. Part of cranidium, GSM Zs183, Garwood Coll. Wenlock Shale, Dolyhir, Radnorshire. Right oblique view showing contact of lateral glabellar lobe 2p with fixed cheek and contrast in size of tubercles of fixed cheek and glabella, x 6.4. See also Pl. 6, figs. 6, 10, 11.

5. Rostral plate, DJS/6a, Wenlock Shale, lundgreni Zone, main sunken road, Burrington, Herefordshire. Ventral view, x 4.5.

6, 9. Hypostome, LM 4677, Wenlock Shale, sunken road, Burrington, Herefordshire. Oblique stereo-pair, ventral view, x 5.

7

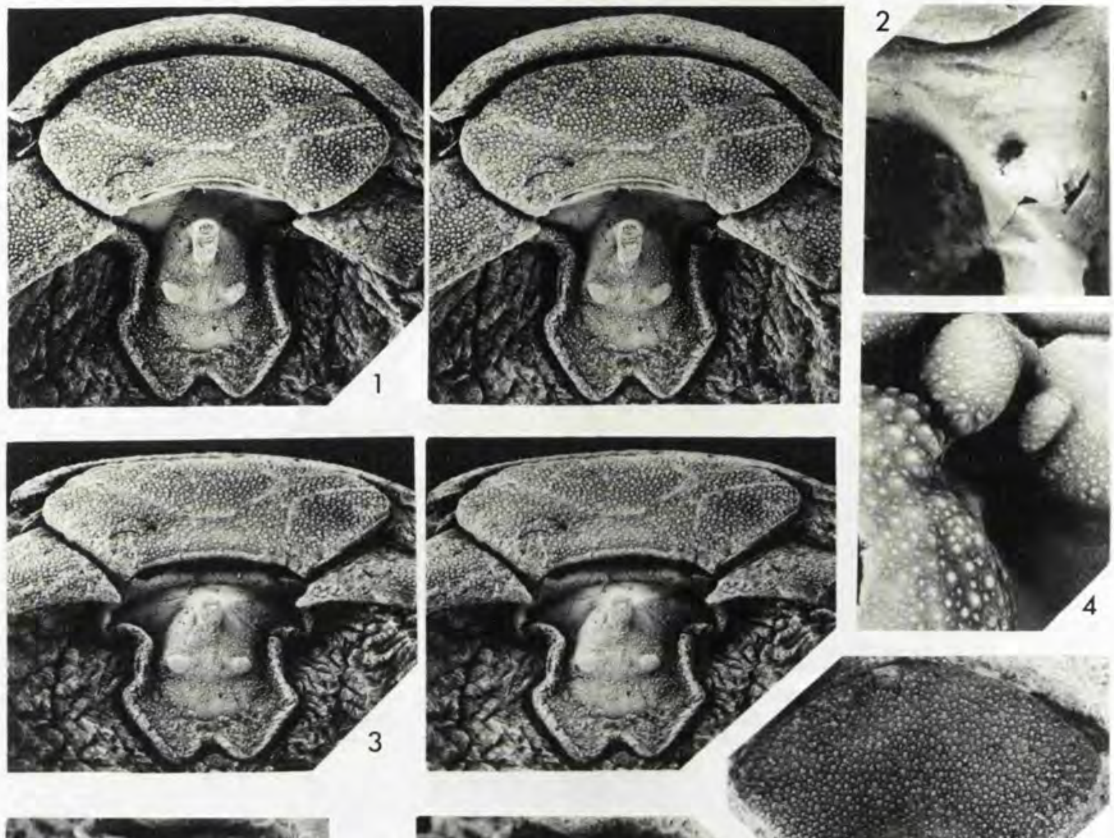


PLATE 8.

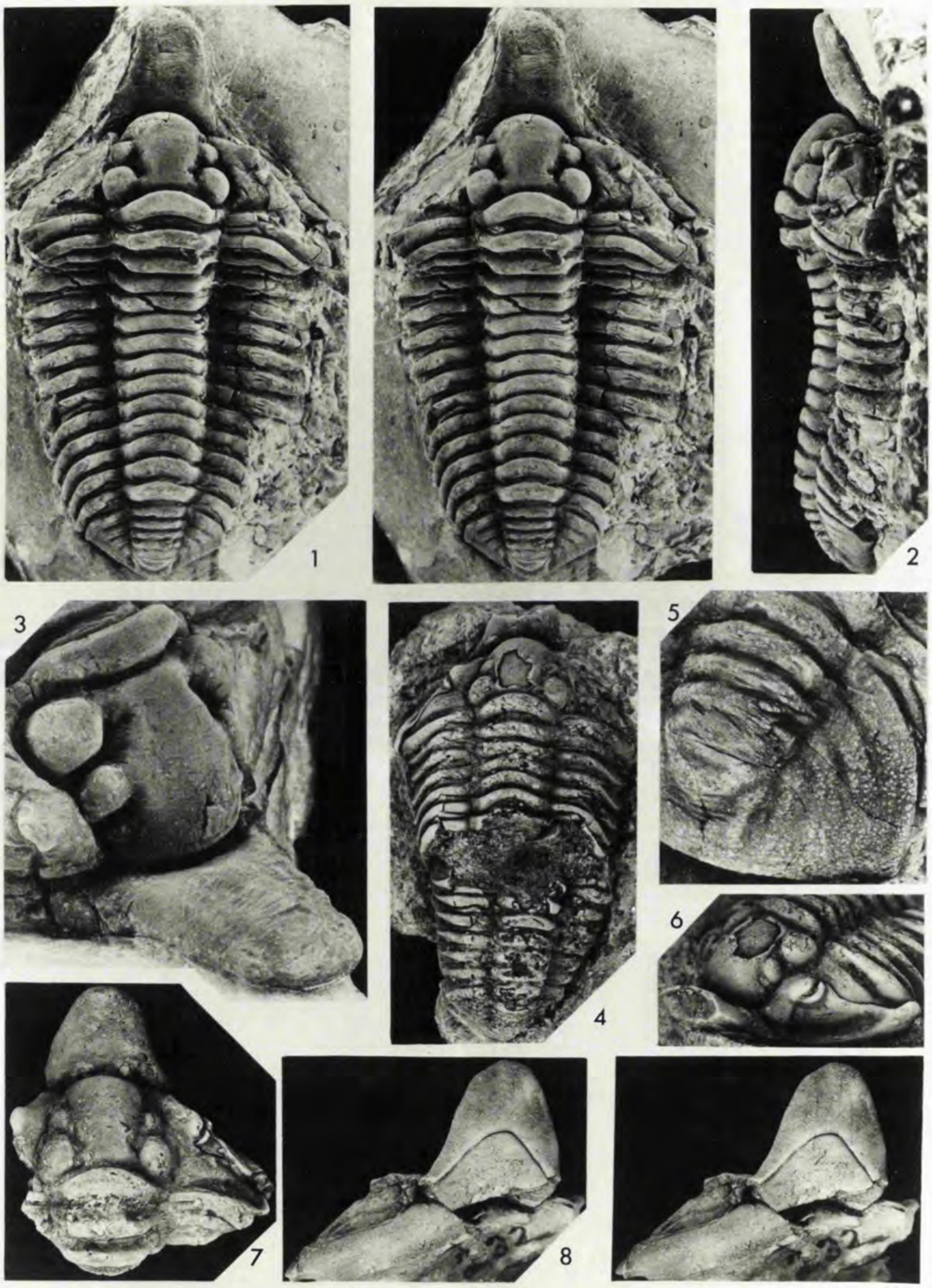
Figs. 1-8. Spathacalymene nasuta (Ulrich, 1879)

1-3, 5. Almost complete individual, USNM 170363, Dr. J.F.Cutler informs me that Tillman's (1960) paper contains erroneous information about the collecting locality of this specimen. It should read "Osgood Limestone, quarry just east of Napoleon, Ripley County, Indiana, U.S.A." Coll. Dr. J.F. Cutler. Figured Tillman 1960, pl. 116, figs. 1, 4, 5, 8, 9. Dorsal stereo-pair, right lateral view, x 1; right oblique view of cranidium x 2; right oblique view of pygidium, x 3.3.

4, 6. Lectotype, subsequently designated by Tillman 1960, p. 893, pl. 116, figs. 2, 3, 6, 7. Almost complete individual, USNM 41871 (one of seven original syntypes of Ulrich having this USNM number), Osgood Formation, Osgood, Indiana, U.S.A. Dorsal view, x 1.5; left oblique view of cephalon, x 1.8.

7, 8. Paralectotype, incomplete cranidium with the remains of two thoracic segments, USNM 41871, Osgood Formation, Osgood, Indiana, U.S.A. Figured Tillman 1960, pl. 116, figs. 10-12. Dorsal view, ventral stereo-pair, x 1.5.

8



APPENDIX 1

MEASUREMENTS TAKEN ON CALYMENIDS

IN CHAPTERS A, B, D-F.

A star (*) indicates an estimated measurement.

A letter (d) indicates a measurement which has been doubled.

(S) = steinkern.

(C) = cast.

(S/E) = partially exfoliated specimen.

<u>Pharostoma</u> <u>vokovicense</u> Snajdr, 1956

	NMP 184/67 (S)	BM I5408 (S)	BM It187 (S)
A	14.4		12.4
B	11.3		9.7
B1	9.1	5.7*	7.7
B2	2.4		
C	7.3		6.2
D	3.1	1.9	2.7
D1	1.7	0.8	1.1
I	35.1d		
J	14.5	8.5	12.3
J1	17.0		
K	13.5		11.1
K1	13.3	8.0	11.1
K2	10.8	6.9	9.5
K3	7.5	5.1	6.9
K5	7.2	4.6	6.3

Pharostoma pulchrum pulchrum (Beyrich, 1846)

	MB 501 B.K. (S)	MB 303 B.K. (C)	MB 264 B.K. (S)	NMP It327 (S)	BM In31919 (S)	BM In31920 (S)
A		18.3*			12.4	18.9
B	13.8	13.9		13.6	9.2	15.0
B1	11.0	11.1		11.1	7.4	12.2
B2	2.1					
C	7.8	7.5		7.5	5.4	8.3
D		4.4			3.1	3.9
D1		1.6		2.0	1.2	1.6
I	34.9d				28.0d	
J	21.4	19.4			14.0	
J1	23.2	22.4d			16.5	
K	15.0			14.2	10.0	15.0
K1	15.4	15.0d		15.2	10.2	15.5
K2	13.1	13.1		13.0	9.0	14.0
K3	8.7	8.3		8.7	6.1	9.3
K5	8.1	8.0		8.4	5.6	8.7
W			18.7			
X			7.7			
X1			5.3			
Y			8.6			
Z			10.0			

	Pharostoma pulchrum pulchrum (Beyrich, 1846)		Pharostoma pulchrum subsp. nov. A
	BM I665 (S)	BM I5422 (S)	DJS/139 (S)
A	13.9		17.5
B	9.9		13.2
B1	8.7	9.9	10.5
B2			2.1
C	6.0		9.0
D	4.0*	4.0	4.3
D1	1.5	1.4	1.5
I	31.0d		
J			18.5
J1			23.5
K	12.1	12.9	
K1	12.6	13.5	15.2
K2	10.5	12.0	12.7
K3	7.0	7.8	8.0
K5	6.6	7.3	7.6

	<u>Pharostoma</u> aff. <u>P</u>. <u>denticulatum</u> (Eichwald, 1860)	<u>Pharostoma</u> <u>nieszkowskii</u> Schmidt, 1894	
	RM Ar10592	RM Ar34406 (S/E)	RM Ar34361 (S/E)
A	6.0	6.4	4.6
B	4.3	4.6	3.3
B1	3.4	3.5	2.5
C		2.5	1.6
D	1.7	1.7	1.3
D1	0.7	0.8	0.6
I		11.2d	
J		5.6	
J1			4.1
K	4.1	4.5	
K1	4.2	4.5	3.0
K2	3.7	4.0	2.8
K3	2.7	2.8	2.0
K5	2.7	2.8	1.9

<u>Pharostoma</u> <u>simile</u> Thorslund, 1940 | <u>Pharostoma</u> <u>oelandicum</u> Angelin, 1854

	IPU Ar2469	IPU Ar2468	IPU Ar2467	RM Ar9150	RM Ar2285
A	10.5	18.3	5.9	12.2	7.9
B	7.7	13.3	4.3	9.2	6.4
B1	6.1	10.7	3.4	7.5	4.9
B2			1.0		
C	4.1		2.3		2.9
D	2.8	5.0	1.6	3.0	1.5
D1	1.7	3.0	0.9	1.9	0.7
I	21.1		11.0*		
J	10.0	17.0	5.4		8.0
J1	11.3	20.2	6.6		
K	7.1	13.3	3.6	9.0	5.5
K1	7.4	14.4	3.8	9.4	5.7
K2	6.3	12.3	3.7	8.1	5.3
K3		8.0	2.6	5.4	3.9
K5	4.6	7.8	2.6	5.3	3.7
	IPU Ar2476	IPU Ar2478	IPU Ar2473	IPU Ar2474	
W	5.9	11.7			
X	1.8	3.6			
X1	1.0	2.0			
Y	3.1	6.1			
Z	3.3	6.5			
a			7.4	5.0*	
b				5.9	
b1			6.0	4.0*	
b2			6.5	4.3*	
e			6.2		
e1				2.0	

<u>Pharostoma</u> <u>foveolatum</u> (Törnquist, 1884)

	SGU unnumbered	IPU Ar469	IPU Ar465	IPU Ar465	IPU Ar453a
A	14.2	39.7			
B	9.9	25.0*			
B1	8.1	21.5			
B2	2.6				
C		21.2			
D	4.3	14.7			
D1	3.2	11.7			
J	14.2				
K	9.3				
K1	9.5	23.9			
K2	8.8	21.0			
K3	6.6				
K5	6.5	15.5			
W			38.7	40.0*	39.0*
X			12.2	13.0*	12.5
X1			5.9	6.9	6.5
Y			20.0		22.2
Z			22.1		24.5

	Pharostoma ornithoreos sp. nov.			*Pharostoma leptaenarum* (Törnquist, 1884)		
	BM It8931 (S/E)	BM It8934 (S/E)	BM It8930 (S/E)	IPLU L0593t	IPLU unnumbered	IPLU L01938t (C)
A	10.2	6.5	8.4*			6.5
B	7.6	5.0	6.3		4.0	4.2
B1	6.0	4.0	5.2	4.0*	3.3	3.1
C	3.5					2.6
D	2.6	1.6	2.1*	1.3		1.3
D1	1.2	0.7	0.9	0.9		0.7
J	10.1		8.5			
J1	10.1					
K	6.0				3.3	
K1	6.4	4.3	5.9	3.7	3.5	5.1*
K2	5.9	3.4	5.3	3.5	3.2	4.5
K3	4.6	2.9	4.0	2.7	2.5	3.6
K5	4.5	2.8	3.9	2.5	2.4	3.5

<u>Pharostoma</u> <u>obtusum</u> (McCoy, 1846)

	RM Ar47707	RM Ar43612	RM Ar43613	RM Ar43614	RM Ar10688
A	4.9	4.3	3.9	4.7*	6.9
B	3.8	3.4	3.0*	3.7	5.5
B1	3.2	2.8	2.5	3.1	
C	2.1	1.8	1.5		
D	1.1	0.9	0.9	1.0*	1.4
D1	0.5	0.6	0.6	0.6	
J		4.5	3.7	4.5	6.9
J1			4.2	5.1*	
K		2.9	2.4	2.9	4.8
K1		3.0	2.5	3.1	5.1
K2	3.2	2.9	2.4	2.9	4.7
K3	2.4	2.1	1.9	2.3	3.3
K5	2.3	2.1	1.9	2.3	3.3

	Pharostoma cf. P. nieszkowskii Schmidt, 1894		Pharostoma cf. P. foveolatum (Tornquist, 1884)	
	PMO 91024 (2) (S) Oslo-Asker	PMO 91024 (1) (S) Oslo-Asker	PMO 38555 Nes-hamar	PMO 38556 Nes-Hamar
A	3.4*	5.8		
B	2.7	5.1		
B1	2.0	3.4	1.8*	3.2
C	1.2			
D	0.7	1.7		1.9
D1	0.4	1.0	0.4	1.0
I	5.5			
J	2.9	5.8	2.8d	5.4d
J1	3.3			
K1	2.0	4.1	1.8	3.8d
K2	1.8		1.8	3.6
K3	1.3		1.4	2.4
K5	1.3		1.3	2.3

	Pharostoma narinosum sp. nov.			Pharostoma sp. A	
	PMO 81266	PMO 91448	PMO 91449	PMO 81312 (1)	PMO 81312 (2)
	Oslo-Asker	Oslo-Asker	Oslo-Asker	Oslo-Askar	Oslo-Asker
A	21.2*	22.5		4.5	4.0
B	14.1*	14.7	12.8	3.7	3.2
B1	11.8*	12.2	10.3	2.9	2.5
C				1.8	1.6
D	7.1	7.8		0.8	0.7
D1	4.6	5.3		0.3	0.3
I				9.3	
J		21.2		4.8	
J1				5.4	
K			11.7	3.1	
K1			12.4	3.2	
K2			10.5	3.0	
K3			7.1	2.4	
K5			7.0	2.4	

F. Jemtlandica Thorslund, 1940

	PMO 81112/1/1	PMO 81112/1/2	PMO 81112/2/1	PMO 81112/3/1
	Oslo-Asker	Oslo-Asker	Oslo-Asker	Oslo-Asker
A	6.5	6.3*		8.5
B	5.3	5.2		7.1
B1	4.1	4.0	6.5	5.5
C	2.2		3.2	3.3
D	1.2	1.1		1.4
J	4.6d			
J1			12.0*	
K	4.4d	4.6d	7.0	
K1	4.4d	4.6d	7.3	6.4
K2	3.6d	3.8d	6.0	5.3
K3	3.2d	3.4d	4.8	4.4
K5	2.6	2.7d	4.2	3.9

F. jemtlandica Thorslund, 1940

	PMO 91081 Oslo-Asker	PMO 91082 (S) Oslo-Asker	PMO 81112/4/1 Oslo-Asker	PMO 81112/5/1 Oslo-Asker	PMO 81112/5/2 Oslo-Asker
A			6.2	8.0	9.4
B			5.2	6.4	7.7
B1	8.8	6.3	4.2	5.0	6.0
C			2.3		
D	2.0*	1.7	1.1	1.6	1.7
I			12.0d		
J			7.6*		
J1	15.5*				
K1	10.0	7.6*	4.3	5.5	6.8
K2	7.8		3.4	4.5	5.3
K3	6.8		3.0	3.8	4.2
K5	5.5		2.6	3.0	3.7

F. *jemtlandica* Thorslund, 1940

	PMO 81112/6/1 Oslo-Asker	PMO 91076 Oslo-Asker	PMO 91079 Oslo-Asker	PMO 81308 Oslo-Asker	PMO 81218 Ringerike	PMO 81350 Oslo-Asker
A	11.6		7.7	11.8	10.3	12.2*
B	9.5		6.4	9.6	8.5	10.0*
B1	7.5	5.1	5.1	7.8	6.9	8.3
C			2.5	4.0	3.7	
D	2.1	1.3	1.3	2.2	1.9	2.2
I				21.0d		
J			6.1	10.9	7.9	
J1	14.0*		9.2	14.5*	12.1	
K	8.0		5.0	8.7	7.0	8.1
K1	8.2	5.8	5.2	8.8	7.3	8.5
K2	6.8	4.7	4.4	7.4	6.0	7.0
K3	5.7	3.9	3.7	6.4	5.0	6.4
K4				5.6		
K5	5.1	3.3	3.2	5.2	4.3	5.0

F. jemtlandica Thorslund, 1940

	PMO 91085 Oslo-Asker	PMO 80954 Oslo-Asker	PMO 80959 Oslo-Asker	PMO 81147/1 Oslo-Asker	PMO 5836 Oslo-Asker	PMO 6492 Oslo-Asker
A	9.1		11.4	9.2	7.5	10.5
B	7.3		9.4	7.5	6.0	8.6
B1	5.9	9.0	7.6	5.8	4.9	6.8
C	3.2					3.7
D	1.8	2.1	2.0	1.7*	1.5	1.9
I	16.8d					
J	10.6	10.3				
K	6.3	9.6	8.0			7.5
K1	6.7	9.8	8.2	6.1	5.4*	7.8
K2	5.4	8.3	6.5	5.0	4.5	6.2
K3	4.6	6.7	5.6	4.3	3.8	5.2
K5	3.9	5.5	4.7	3.5	3.1	4.3

<u>F.</u> <u>jemtlandica</u> Thorslund, 1940

	PMO 81112/8/1 Oslo-Asker	PMO 81112/9/1 Oslo-Asker	PMO 81112/9/2 Oslo-Asker	PMO 81112/9/3 Oslo-Asker
A		9.7	8.6	7.4
B		8.1	7.1	6.1
B1	8.2	6.5	5.8	4.7
C			2.8	
D	2.1	1.6	1.5	1.3
I			15.8d	
J			7.1	
J1			10.7	
K			6.2	
K1	9.0	7.4	6.3	5.0
K2	7.1	6.0	5.3	4.1
K3	6.0		4.5	3.4
K5	5.1		3.6	2.9

F. *jemtlandica* Thorslund, 1940

	PMO 81112/10/1 Oslo-Asker	PMO 81112/10/2 Oslo-Asker	PMO 81112/10/3 Oslo-Asker	PMO 81112/10/4 Oslo-Asker
A	10.6	6.5	12.3*	
B	8.8	5.4	10.5*	8.5
B1	6.9	4.4	8.5*	6.7
C	3.8			
D	1.8	1.1	1.8	
K	7.7			
K1	8.0	4.8	9.3	7.9
K2	6.6	3.8	7.5	6.5
K3	5.8	3.3	6.5	5.6
K5	4.7	2.7	5.6	4.3

	PMO 81313 Oslo-Asker	PMO 81110/1 Oslo-Asker	PMO 81112/7/2 Oslo-Asker	PMO 5575 Oslo-Asker	PMO 81109 Oslo-Asker
W	9.6	10.4d	11.4	3.8	11.6
X	3.0	3.6	3.9	1.4	3.7
X1	2.0	2.0	2.1	1.0	2.2
Y	3.7	4.7	4.6	1.5	4.8
Z	4.2	5.1	4.9	1.7	5.2

F. jemtlandica Thorslund, 1940

	PMO 81112/10/5 Oslo-Asker	PMO 81112/1 Oslo-Asker	PMO 81112/2 Oslo-Asker
A		7.0	8.8
B		5.8	7.3
B1	8.5	4.5	5.9
D		1.2	1.5
K1	9.0	4.9	6.5
K2	7.7	4.0	5.4
K3	6.5	3.3	4.5
K5	5.4	2.8	3.8

	PMO 81105 Oslo-Asker	PMO 81110/2 Oslo-Asker	PMO 81147/2 Oslo-Asker	PMO 81140 Oslo-Asker	PMO 91084 Oslo-Asker	PMO 5577 Oslo-Asker
a	4.1	4.2	3.5*	4.9	2.8	
b	4.8	4.8	4.2	5.8	3.3	
b1	3.0	3.1	2.7	3.8	2.1	
b2	3.2	3.2	2.7	3.9	2.2	
b3	1.6	1.8	1.4*	2.1	1.2	
d	4.3	4.0*	4.1	5.4	3.0	
e	3.2	3.2	3.1	3.7	2.1	
e1	1.8	1.5	1.1	1.8	1.0	
e2	0.6	0.7	0.4	0.8	0.4	
g						6.0
g1						2.7
h						1.6

F. scabustula sp. nov.

	PMO 81138 Oslo-Asker	PMO 81135 Oslo-Asker	PMO 63421 Oslo-Asker	PMO 91086/1 Oslo-Asker	PMO 91086/2 Oslo-Asker	PMO 81250 Oslo-Asker
A	7.5	6.9	8.5	11.3	9.0	7.8
B	6.1	5.6	7.0	9.2	7.4	6.3
B1	4.6	4.4	5.5	7.3	5.9	4.8
C	2.7	2.4				2.9
D	1.4	1.3	1.5	2.1	1.6	1.5
I	13.2d	12.8				13.9
J	6.5	5.3			7.5	5.5
J1	9.0d	8.1				8.8
K	5.5	4.6				5.2
K1	5.7	4.8	7.1	8.4	6.1	5.4
K2	4.8	3.9	5.7	6.6	5.2	4.3
K3	4.1	3.4	5.0	5.6	4.1	3.7
K5	3.3	2.8	4.0	4.7	3.5	3.0

F. scabustula sp. nov.

	PMO 5491 Oslo-Asker	PMO 20444 Oslo-Asker
A	9.6	6.2
B	8.0	5.1
B1	6.2	3.9
C	3.6	
D	1.6	1.1
I	19.2d	
J	9.2	5.2
J1	12.7	
K	8.0	4.5
K1	8.3	4.7
K2	6.8	4.0
K3	5.4	3.5
K5	4.7	2.8

	PMO 81256 Oslo-Asker	PMO 5380 Oslofiord
W	8.7	2.5
X	3.4	0.9
X1	2.0	0.7
Y	3.8	1.0
Z	4.4	1.1

	PMO 91093 Oslo-Asker	PMO 81251 Oslo-Asker
a	5.4	3.4
b	4.6	4.2
b1	3.5	2.5
b2	3.3	2.4
b3	2.0	1.3
d	5.1	3.6
e	4.0d	3.1
e1	2.0	1.4
e2	0.6	0.4

	PMO 91092 Oslo-Asker
g	7.5
g1	3.2
h	1.7

<u>Gravicalymene</u> <u>capitovata</u> sp. nov.

	PMO 91061 (C)	PMO 82681 (S)	PMO 60414 (S)	PMO 60418/1 (S)	PMO 60418/2 (S)	PMO 66598 (S)	PMO 91045 (C)	PMO 91051 (C)	PMO 91036 (C)
A	12.5	15.7		7.2					
B	9.3	12.0	10.0	6.1			12.9		
B1	7.2	10.0	8.0	5.0	5.3	8.6	10.1		
B2	1.4		1.2	0.7	1.8				
C	5.4	6.3	5.5	2.8			7.9		
D	3.2	3.6		1.1	1.4				
D1	0.6	0.4	0.8	0.3	0.4	0.5			
I	26.2		31.2						
J		11.5	10.9*	6.1	6.0	10.3*			
J1	15.5	17.6*		10.0			21.2		
K		11.1*							
K1	9.3*	11.1	10.2	6.0*	5.5	10.1	13.0		
K2	6.5	8.2	6.4	4.4	3.7	7.5	9.2		
K3	5.5	7.3	5.5	3.8	3.2*	6.0	8.5		
K5	5.1	6.3*	5.0	3.2*	3.0	5.2*	6.9		
a								7.6	
b								10.5	
b1								6.3	
b2								6.3	
d								7.7	
e								6.6	
e1								4.2	
g									9.6
g1									5.0*
h									3.3

<u>Quadricalymene</u> <u>lirella</u> gen. <u>et</u> sp. nov.

	PMO 82528 (S) Eiker-Sandsvaer	PMO 91073 (S) Eiker-Sandsvaer	PMO 91072 (S) Eiker-Sandsvaer	PMO 82466 (S) Eiker-Sandsvaer
A	4.6	3.5	5.6*	5.5*
B	4.1	3.1	5.0	4.9
B1	3.3	2.5	4.0	3.9
B2	0.7*		0.9	0.7
C	1.5	1.2	1.9	1.9
D	0.5	0.3	0.6	0.6
I	10.2	7.0d	12.6*	13.3
J	3.8	2.6*	4.7*	5.3
J1	5.9	4.0*	8.5	8.6d
K	3.5	2.5	4.7	4.7
K1	3.5	2.5	4.7	4.6
K2	2.6	1.7	3.5	3.8
K3		1.7	3.3	3.4
K5	2.4	1.6	3.3	3.3

<u>Quadricalymene</u> <u>lirella</u> gen. <u>et</u> sp. nov.

	PMO 82465 (S) Eiker-Sandsvaer	PMO 91068 (S) Eiker-Sandsvaer	PMO 91067 (S) Eiker-Sandsvaer	PMO 81919 Oslo-Asker
A	3.0	5.3	2.7	3.5
B	2.7	4.8	2.4	3.3
B1	2.2	3.8	1.9	2.5
B2		0.7*		
C	1.0*	1.8	0.7*	1.4
D	0.3	0.5	0.3	0.2
I	6.0d		5.4d	8.2
J	2.4*	4.6		3.0
J1	3.8*	7.4*		5.6
K	2.0	4.2	1.6	3.4
K1	2.1	4.2	1.6	3.3
K2	1.6	3.3	1.3	2.6
K3		3.1	1.2	2.5
K5	1.6	3.0	1.2	2.5

Diacalymene drummuckensis (Reed) 1906

	BM In41013	BM In23370	RSM 1957.1.2546	RSM 1958.1.2549	RSM 1958.1.2553
	(S)	(S/E)	(S)	(S)	(S)
A	18.5	14.8	19.6		15.4*
B	15.5	12.6	16.5		13.2
B1	12.4	9.5	13.6	9.6	10.8
B2		1.7		1.9	2.4
C		5.2	.	.	
C1		8.8	12.0	9.0	
D	3.0	2.2	3.1	2.6	2.2*
D1		0.7	1.6	1.4	0.8*
J		13.4	17.0*	15.8	
J1		16.8		16.8*	17.2
K	11.0	11.0	12.0	11.0	
K1	12.6	12.0	13.3	12.0	12.3
K2	11.0	9.9	10.6	10.9	10.3
K3	8.9	8.5	9.2	8.8	9.0
K5	7.8	7.5	8.5	8.1	8.4

<u>Diacalymene drummuckensis</u> (Reed) 1906

	RSM 1957.1.579 (S)	WM unnumbered (S/E)	RSM 1968.50.34A (S/E)	RSM 1968.50.34B (S)	RSM 1899.91.11A (S)
A	15.7		16.3*		15.0
B	13.3		13.1	9.3	12.5
B1	11.2	14.5*	10.6	7.5	10.0
B2	2.1	3.5	1.9	1.0	1.9
C	6.5				
C1	10.5		9.3	6.6	9.0
D	2.4	3.7	3.2		2.5
D1	1.0	0.9	1.0		0.9
J	16.0	20.6	15.5		14.0
J1	20.0	25.3	17.0d	13.9	17.3
K	12.7		12.0	9.2	11.0
K1	12.9	17.2	12.2	10.0	12.0
K2	10.8	14.9	11.3	8.8	10.2
K3	9.1	12.6	9.2	7.3	8.5
K5	8.0	11.9	8.4	6.7	7.5
g					10.9
g1					6.4
h					2.2
p					1.2

Diacalymene drummuckensis (Reed) 1906

	RSM 1957.1.576 (S)	HM A3612 (S)	HM A3114 (S)	HM A3115 (S)	HM A3110 (S)	HM A973 (S)	HM A5411 (S)	HM A5412 (S)	HM A5413 (S)
A	13.9	11.4*	18.8	12.5		15.6	11.6		
B	12.0	9.7*	15.7	10.7		13.5	9.6	9.7	14.7
B1	9.9	8.1	13.0	8.7	8.0	11.0	7.6	7.7	12.0
B2	2.0	1.3	2.6	1.8	1.2		1.7	1.5*	2.1
C	5.7				5.0		4.7		
C1	8.9	7.0		7.9	7.3		7.0		
D	1.9	1.7	3.1	1.8		2.1	2.0		
D1	0.8	0.7	1.3	0.6		1.3	0.9		
J	15.0d	10.8*	19.0*	12.0		15.7	10.5		
J1	18.0d	13.0	19.7d	13.8	14.8d	19.0d	13.8d		21.0d
K	11.5		13.0	8.7	9.1	10.2	8.4		12.0
K1	11.7	9.4	13.7	9.6	9.8	12.1	8.7	8.6	13.3
K2	10.2	8.1	12.2	8.0	8.3	10.3	7.5	7.3	12.0
K3	9.0		10.0	6.9	7.1	8.5	6.3	6.5	10.2
K5	8.1		9.5	6.3	6.6	7.5	5.8	5.9	9.5

<u>Diacalymene</u> <u>drummuckensis</u> (Reed) 1906

	HM A3128 (S)	HM A4131 (S)	HM A5085 (S)	HM A910 (S)	BU 7 (S)	BM In23383	HM A5081 (S)	RSM 1968.50.35 (S)
A					18.6*		10.5	
B	12.5*	12.5		13.0	15.7*		9.0	8.2*
B1	10.3	9.5	11.0*	10.5	12.7		7.1	6.5
B2		1.5	2.2	2.5	2.5		1.3	
C		6.0		6.8				3.5*
C1	9.5*	8.6	10.3	9.6	11.4		6.2	
D			2.5		2.9*		1.5	
D1			1.1		1.3		0.4	
J		13.6	17.5	15.5			12.1	9.5
J1	16.0d	17.0	21.4d	17.7			10.1	12.3
K	10.2	11.0	13.0	12.0	11.7		8.0	7.9
K1	11.4	11.6	13.8	12.2	13.0		8.5	8.4
K2	9.1	9.8	11.7	10.1	10.6		7.2	6.9
K3	8.1	8.3	10.3	8.5	9.1		6.0	5.7
K5	7.5	7.5	9.0	8.0	8.2		5.6	5.2*
W		11.9				32.5	11.7	
X		4.8				14.0	4.5	
X1		2.6				8.0	2.7	
Y		5.5				16.9	6.7	
Y1						3.9		
Z		5.8				18.1	7.0	

<u>Diacalymene</u> <u>drummuckensis</u> (Reed) 1906

	HM A910 (C)	HM A758 (S)	HM A556 (S)	HM A759 (C)	BM In23381 (C)	GSM 70671	BM In43029
A							23.7
B						14.0	19.6
B1						11.3	16.2
B2						2.5	3.1
C						6.6	8.7
C1						10.2	14.7
D							4.1
D1							1.6
J							21.5*
J1						19.0d	26.6
K						13.3	17.4
K1						14.0	18.3
K2						12.0	15.5
K3						10.2	12.9
K5						8.9	11.5
a		7.5	3.4	5.6	6.1		
b		8.5	4.0	6.6	7.4		
b1	8.7	6.0	2.5	4.3	4.7		
b2	8.3*		2.5	4.3			
b3	4.2	3.1	1.3	2.2	2.4		
d	12.8	10.0	3.9*	5.8d	6.7		
e	9.0d	6.4	3.2	4.3	4.7		
e1		2.8	1.6	1.5	2.0		
g					8.6		
g1					4.0		
h					2.3		

<u>Diacalymene</u> <u>Crassa</u> Shirley, 1936

	GSM	SM	GSM	BM	BM	SM	GSM
	54910	A54095	54911	It8647a	In58236a	A32717	TCC1941
	(S)	(S)	(S)	(S)	(S)	(S)	(C)
A				14.4	12.2	13.5	13.0*
B				11.7	10.0	10.8	10.5*
B1	9.5*	10.3	9.0*	9.5	8.0	8.8	7.8
B2	1.6*		1.7			1.6	
C					4.5	6.3	
C1	8.0*	9.2	7.2*	8.0		7.1	
D	3.5	3.9	2.6	2.7	2.2	2.7	2.5*
D1	1.0*	1.2	0.6			0.8*	0.5*
I					25.4d		
J	13.9		12.8	14.5		13.1	
J1	14.6*		13.5	16.0	12.6	16.0	13.9
K	9.6			11.2	8.4	8.9	9.3
K1	10.7	12.9	9.5	10.8	8.8	10.4	9.5
K2	8.8	10.5	8.1	8.5	7.5	8.3	7.3
K3	7.2	9.0	7.0	7.3	6.2	6.7	6.5
K4	6.6		6.5		5.5		
K5	6.3	7.6	6.3	6.6	5.4	6.2	
W					13.5		
X					5.0		
X1					3.5		
Y					6.5		
Z					7.3		

Diacalymene consimilis (Cooper, 1930)

	BM It7393	BM It7392
A	14.0	
B	11.4	13.1
B1	9.0	10.1
B2	2.0	2.0
C	5.4	6.7
C1		9.9
D	2.6	
D1	0.7	
I		30.0
J		14.5d
J1	16.6d	17.5
K	10.2	12.0
K1	11.4	12.9
K2	9.0	10.4
K3	7.3	8.7
K5	6.4	7.4

Diacalymene gibberosa sp. nov.

	PMO 20948	PMO 20945	PMO 41624	PMO 41620	PMO 41626 (S/E)
A	8.8	6.2	7.7	10.7	
B	7.1	5.0	6.1	8.5	
B1	5.4	3.9	4.7	6.7	6.6
B2	0.7	0.6	0.7	1.0	
C	3.2	2.4	3.1		4.7
D	1.7	1.2	1.6	2.2	2.0
D1	0.8	0.4	0.7	1.0	1.0
I	21.0d	13.6	16.5		
J	9.4	6.2	8.0		
J1	11.5	7.6	9.2		
K	6.9	4.5	5.7		
K1	6.4	4.3	5.3	7.0d	
K2	5.9	4.1	5.0	6.6	6.3
K3	4.9	3.3	4.0	5.3	5.0
K5	4.2	2.9	3.6	4.6	4.5

	PMO I0838	PMO 20945	PMO 41620
W	15.8	12.3	5.0
X	5.9	4.7	1.9
X1	3.5	2.3	1.2
Y	5.8	4.4	1.8
Z	6.3	5.0	2.1

	PMO 41634 (C)
a	3.2
b	3.5
b1	2.3
b2	2.3
b3	1.2
d	3.5
e	2.3*
e1	1.1*

C. frontosa Lindström, 1885

	RM Ar27059 Visby	RM Ar27072 Visby	RM Ar6210 Visby	RM Ar6211 Visby	RM Ar6212 Visby	RM Ar42807 Visby
A		10.6	10.3			10.5
B	7.5	8.9	8.4	8.7	10.1	8.5
B1	6.0	7.1	6.6	7.0	7.9	6.6
B3		1.3	1.5	1.6		1.6
B4	2.1	2.4	2.5	2.6		2.4
C		4.4*	4.3	4.2		4.2
D		1.7	1.9			2.0
I			18.4			18.6
J		9.2	12.6			9.5
J1		12.7				12.8
K			7.3	7.4	8.3	7.3
K1	6.2	7.3	7.5	7.4	9.1	7.5
K2	5.3	6.1	6.5	6.4	7.8	6.8
K3	4.4	5.2	5.1	5.2*	6.4	5.6
K5	4.2	5.0	5.0	4.9*	5.8	5.3
W	7.5	8.7	9.6			
X	3.7	4.4	4.3			
X1	1.8	2.4	2.2			
Y			4.3			
Z	3.4	4.5	4.7			
g						7.3
g1						3.0
h						2.1
p						1.0

C. frontosa Lindström, 1885

	RM Ar42808 Visby	RM Ar27037 Visby	RM Ar27038 Visby	RM Ar27039 Visby	RM Ar27040 Visby	RM Ar27041 Visby
A		12.2	11.9	12.0	10.9	
B	9.2	10.2	9.5	8.4	9.0	9.5
B1	7.0	8.2	7.6	6.6	7.0	7.6
B3	1.9	1.6	1.6		1.4	1.6
B4	2.8	2.8	2.3		2.5	2.8
C	4.6	5.5	4.6		4.5	4.8
D		2.0	2.4	1.9	1.9	
I			19.7		17.5*	19.8
J		10.5	11.1	8.5	9.6	
J1		14.8	14.2		12.9	14.1
K	7.7	8.5	8.4	7.0	7.5	7.9
K1	7.8	8.8	8.7	7.3	7.7	8.5
K2	7.0	7.8	7.5	6.3	6.7	7.3
K3	5.6	6.3	5.9	5.1	5.4	5.9
K4					5.2	
K5	5.4	5.8	5.7	4.8	5.0	5.3
W		10.4				
X	5.0	5.4	5.5	4.5	4.8	
X1	2.5	2.4	2.9	2.1	2.2	
Y				4.6		
Z		5.4		5.0		
g		7.9	8.7		7.5	
g1		3.6	3.8		3.3	
h		2.1	2.5		2.4	
p		0.9	0.9			

C. frontosa Lindström, 1885

	RM Ar27043 Visby	RM Ar27044 Visby	RM Ar27049 Visby	RM Ar27050 Visby	RM Ar47000 Visby	RM Ar47003 Visby
A		10.9	8.4	7.9	12.6	9.0
B	8.6	9.1	6.6	6.2	10.4	7.3
B1	6.8	7.1	5.1	4.7	8.1	5.8
B3	1.5	1.4	1.3	1.2*	1.6	1.4
B4	2.4	2.5	1.8	1.8	2.9	2.0
C	4.0		3.3	3.2	5.0	3.5
D		1.8	1.8	1.7	2.2	1.7
I	17.9	18.0	14.8		22.2	
J		9.6	7.8	6.9	10.7	7.9
J1	12.2	10.9	10.0	8.9	14.6	10.5
K	7.0	7.5	5.8	5.1	8.3	6.1
K1	7.5	8.0	5.8	5.4	9.0	6.3
K2	6.7	7.1	5.1	4.5	8.1	5.6
K3	5.5	5.7	4.2	3.7	6.3	4.5
K5	5.0	5.3	4.0	3.5	6.0	4.3
X		4.8	3.6		5.3	
X1		2.1	1.5		2.8	
g		7.5	5.5		8.1	
g1		3.3	2.2		3.1	
h		2.0	1.8		2.3	
p		0.6			0.7	

C. *frontosa* Lindström, 1885

	RM Ar47004 Visby	RM Ar47005 Visby	RM Ar47006 Visby	RM Ar47007 Visby	RM Ar47008 Visby	RM Ar47009 Visby
A	7.5		10.8	11.3		7.7*
B	6.4	8.2	8.6	9.1	9.5	6.1*
B1	5.0	6.4	6.8	7.3	7.3	4.5
B3	1.1	1.2				1.0*
B4	1.8	2.3		2.5		1.8
C	3.2		4.4			3.1
D	1.5		2.2	2.2		1.6
J	7.5		9.8	10.2		7.1
J1	9.6		13.2			9.1
K	5.2	6.6	7.4	7.7		5.3
K1	5.5	7.0	7.4	8.0	8.1	5.4
K2	5.6	6.0	6.3	6.8	7.1	4.6
K3	4.2	4.7	5.2	5.8	5.8	3.8
K5	3.9	4.5	4.9	5.4	5.5	3.6
X				4.8		
X1				2.1		
g				8.3		
g1				3.6		
h				2.0		
p				1.0		

C. frontosa Lindström, 1885

	RM Ar47010 Visby	RM Ar47011 Visby	RM Ar47012 Visby	RM Ar27067 Visby	RM Ar27066 Visby	RM Ar27045 Visby
A		9.7	5.8			11.3
B	7.7*	7.8	4.5	8.4	9.0*	9.1
B1	5.9	5.9	3.5	6.6	6.9	7.0
B3	1.2		0.8	1.5	1.5	1.7
B4	2.2		1.2	2.5	2.6	2.6
C			2.2	4.5	4.2	4.7
D		1.9	1.3			2.2
I					18.5	18.9
J		9.2	4.9			10.2
J1			6.5		12.1	13.0
K	6.6	7.0*	3.6	7.4	7.2	7.4
K1	6.6	7.0*	3.7	7.8	7.7	7.5
K2	5.7	6.1	3.2	6.7	6.7	6.8
K3	4.8*	5.0*	2.8	5.3	6.0	5.7
K4				5.0		5.3
K5	4.6*	4.8*	2.5	4.8	5.5	5.1

C. frontosa Lindström, 1885

RM Ar27054

Gotland

a	4.9
b	6.4
b1	4.2
b2	4.0
b3	2.2
d	6.3
e	4.0
e1	1.8*
e2	0.3

<u>Calymene</u> sp. nov.?

	RM Ar27058 Visby	RM Ar27060 Visby	RM Ar27071 Visby	RM Ar27052 Visby	RM Ar27046 Visby	RM Ar27047 Visby
A	13.7	13.3	13.4	11.1	10.9	12.6
B	11.41	11.0	10.9	8.6	8.5	9.6
B1	8.9	8.6	8.5	6.8	6.7	7.4
B3	2.2	2.0	1.9	1.7	1.7	1.6
B4	3.4	3.4	3.1	2.9	2.5	2.7
C	5.5	5.5	5.4	3.9	4.5	
D	2.3	2.3	2.5	2.5	2.4	1.9
I	23.7	23.6	23.3		19.3	
J	12.6	11.7	12.3	10.4	9.8	9.6
J1	16.1	15.5	15.2	12.9	12.7	
K	9.6	9.7	8.8	7.7	7.3	7.7
K1	10.0	10.2	9.3	8.5	7.7	8.0
K2	8.4	8.4	7.9	7.6	6.3	7.4
K3	7.4	7.5	7.1	6.3	5.6	5.7
K5	7.2	7.0*	6.4	6.0	5.4	5.5
W	10.6	10.2	10.3			
X	5.8	5.8	5.6			4.9
X1	3.1	2.8	3.3			2.1
Y			5.2			
Z	5.5	5.4	5.6			
g				8.6*	7.8	
g1				3.2*	3.1	
h				2.6	2.6	
p				0.8		

Calymene sp. nov.?

	RM Ar27048 Visby	RM Ar27042 Visby	RM Ar47001 Visby	RM Ar47013 Visby	RM Ar47014 Visby	RM Ar47002 Visby
A	8.7	11.2	8.4	10.6	5.6	10.0
B	6.8	9.0	6.8	8.7	4.5	8.0
B1	5.2	6.9	5.3	6.7	3.4	6.2
B3	1.2	1.7				1.5
B4	1.8	2.5				2.4
C	3.5	4.7	3.4	4.5		
D	1.9	2.2	1.6	1.9	1.1	2.0
I	15.6	19.5*				
J	8.3	10.4	8.0			9.2
J1	9.9	13.0	10.0			12.1
K	5.8	7.8	5.8	7.6	3.6	7.1
K1	6.1	8.0	6.1	8.0	3.6	7.4
K2	5.2	6.8	5.2	6.6	3.3	6.2
K3	4.4	5.8	4.5	5.7	2.8*	5.2
K4	4.1	5.4		5.2		
K5	4.0	5.2	4.1	4.9	2.6*	5.2
X	3.5					
X1	1.5					
g	6.4					7.2
g1	2.5					3.0
h	2.1					2.4
p	0.9					0.9

<u>Calymene</u> sp. nov.?

	RM Ar27063 Visby	RM Ar27068 Visby	RM Ar27062 Visby	RM Ar47861 Hablingbo ?	RM Ar47866 Hablingbo ?	RM Ar47862 Hablingbo ?
A	10.6	11.1	13.8	12.4	12.8	7.1
B	8.3	9.2	11.1	9.8	10.4	5.5
B1	6.6	7.4	8.8	7.7	8.1	4.2
B3	1.7	2.0	2.0	2.0	1.9	1.1
B4	2.5	2.8	3.1	2.8	3.1	1.5
C	4.0	4.4*	5.5	4.9		2.5
D	2.3	1.9	2.7*	2.6	2.4	1.6
J			12.0		12.0	6.0
J1			15.9	13.8	15.2	
K	6.8	7.4	9.1	8.3		4.6
K1	7.2	8.2	9.5	8.7	9.3	4.5
K2	6.1	6.8	7.9	7.7	7.8	4.0
K3	5.2	5.7	7.0	6.4	6.4	3.1
K4		5.5		6.0		
K5	4.9	5.3	6.7	5.8	6.2	2.8
g						4.8
g1						1.9
h						1.5
p						0.7

Calymene sp. nov.?

	RM Ar27073	RM Ar47865
	Visby	Hablingbo ?
A	13.4	
B	10.4	
B1	8.0	5.0
B3	2.0	1.2
B4	3.1	1.7
C	5.6	2.9
D	3.0	1.9
I	23.9	
J	12.2	7.2
J1	15.5	
K	9.5	
K1	9.4	5.4
K2	8.1	4.6
K3	7.1	3.8
K4	6.2	
K5	6.0	3.4
a	5.6	
b	8.0	
b1	5.1	
b2	4.7	
b3	2.6	
d	7.7	
e	5.0	
e1	2.2	
e2	0.3	

C. tuberculosa Dalman, 1827

	RM Ar47710 Gotland	RM Ar31451 Djupvik	RM Ar47850 Djupvik	RM Ar47846 Djupvik	RM Ar47849 Djupvik	RM Ar47847 Djupvik
A	10.5	8.5	10.0	8.7	10.9	13.9
B	9.7	7.8	9.4	8.0	10.0	12.8
B1	7.5	6.0	7.1	6.3	7.6	9.9
B3	2.3	2.0	2.1	2.1		3.1
B4	2.8	2.2	2.6	2.2		3.5
C	4.5		4.3			
D	0.8	0.7	0.6	0.7	0.9	1.1
I	22.4d	18.6				
J	10.3	7.5		7.7*	10.1	13.1
J1	14.6	11.6				
K	8.6	6.3	8.2	6.7	9.0	11.0
K1	8.4	6.2	8.0	6.7	8.6	11.1
K2	8.0	5.8	7.1	6.0	7.8	10.4
K3	6.2	4.7	5.8	5.0	6.1	8.0
K5	6.0	4.6	5.6	4.9	5.9	7.9
g	7.8					
g1	4.0					
h	2.7					
p	1.0					

C. tuberculosa Dalman, 1827

	RM Ar28445 Djupvik	RM Ar47808 Gotland	RM Ar6229 Djupvik	RM Ar6232 Djupvik	RM Ar6231 Djupvik	RM Ar28444 Djupvik
A	6.6	11.7	5.1	6.3	7.6	3.4
B	6.2	10.9	4.7	5.8	7.0	3.2
B1	4.8	8.4	3.6	4.5	5.4	2.5
B3			1.2	1.3	1.6	0.8
B4		3.1	1.3	1.6	1.9	0.8
C		4.0	1.8	2.3	2.8	1.2
D	0.4	0.8	0.4	0.5	0.6	0.1
I	12.7		11.2	12.7	15.5	6.3
J	6.0		4.7	5.6	7.0	2.8
J1	8.7		7.1*	7.9	10.1	4.5
K	5.1		3.9	4.6	5.6	2.4
K1	5.2	9.7	3.9	4.7	5.5	2.5
K2	4.8	8.4	3.6	4.3	5.2	2.3
K3		6.6	3.0	3.6	4.2	2.0
K5	3.6	6.5	2.9	3.4	4.1	2.0
W			4.9	5.0	6.6	
X			2.1	2.5	3.4	
X1			1.4	1.5	1.8	
Y			2.1	2.2	2.8	
Z			2.2	2.4*		
g			4.2	4.8	5.8	
g1			2.0	2.5	3.1	
h			1.4	1.6	1.7	
p			0.3	0.5	0.6	

C. tuberculosa Dalman, 1827

	RM Ar28446 Djupvik	RM Ar28447 Djupvik	RM Ar28448 Djupvik	RM Ar28449 Djupvik	RM Ar31452 Djupvik	RM Ar28090 Djupvik
A	6.0*	7.3	8.2	5.1		8.0*
B	6.1	6.9	7.7	4.8		7.3*
B1	4.6	5.3	5.9	3.6	8.5*	6.2*
B3		2.0	2.2	1.3	2.3	2.2
B4	1.7					
C	2.5	2.8	3.0	1.7	4.8	3.5
D	0.4*	0.4	0.5	0.3	0.9	0.7
I	12.8					18.9
J	5.5	7.0		4.3	11.0	8.7
J1	8.4	9.8		6.5	15.6	12.0
K	4.9	6.0	6.5	3.7	9.8	6.7
K1	4.8	6.0	6.4	3.8	9.5	6.7
K2	4.3	5.6	5.6	3.5	8.4	6.4
K3	3.6	4.2	4.5	2.8	6.5	5.3
K5	3.5	4.1	4.5	2.7	6.4	5.2
g		3.1				
g1		1.5				
h		1.1				

C. tuberculosa Dalman, 1827

	RM Ar27964 Djupvik	RM Ar27965 Djupvik	RM Ar27966 Djupvik	RM Ar27967 Djupvik	RM Ar27968 Djupvik	RM Ar27969 Djupvik
A	5.2	5.8	5.0	4.7*	5.0	5.8
B	4.9	5.3	4.7	4.4*	5.4	5.3
B1	3.8	4.0	3.5	3.3	3.5	4.0
B3		1.3	1.1	1.0	1.0	1.2
B4		1.4	1.3	1.2	1.3	1.4
C		2.0	1.8		2.0	2.2
D	0.3	0.5	0.3	0.3	0.4	0.5
I		12.5	10.7d	9.5	11.2d	11.4d
J	4.4*	5.5	4.3		4.5	4.8
J1		7.0	6.8	6.3	6.8	7.4
K	3.9	4.2	3.9	3.5	4.0	4.1
K1	3.8	4.1	3.9	3.6	3.9	4.2
K2	3.3	3.5	3.3	3.1	3.5	3.7
K3	2.8	3.0	2.9	2.5	3.0	3.2
K5	2.7	3.0	2.8	2.3	2.9	3.1
W	4.4				4.3*	
X	2.1				2.0	
X1	1.3				1.2	
Z	1.9				1.2	
g					3.6	
g1					1.7	
h					1.3	
p					0.4	

<u>C. tuberculosa</u> Dalman, 1827

	RM Ar27970 Djupvik	RM Ar27971 Djupvik	RM Ar26972 Djupvik	RM Ar27973 Djupvik	RM Ar27974 Djupvik	RM Ar27975 Djupvik
A	4.7	4.7	5.4	5.3	5.5	4.2
B	4.4	4.4	5.0	4.9	5.1	4.0
B1	3.3	3.4	3.8	3.8	3.9	3.2
B3	1.0			1.2	1.3	1.0
B4	1.2	1.2	1.3	1.3	1.4	1.1
C	1.8	1.9	1.8	1.8	2.1	1.6
D	0.3	0.3	0.4	0.4	0.4	0.2
I	9.9	8.8d	11.0d	10.2d		8.5
J	4.3		4.7		4.9	3.4
J1	6.4*		7.2*		7.4	5.7
K	3.4	3.5	4.1	3.9	4.1	3.[illegible]
K1	3.5	3.5	4.1	4.0	4.2	3.2
K2	3.1	3.2	3.7	3.7	4.0	3.2
K3	2.7	2.7	3.1	3.1	3.1	2.6
K5	2.6	2.6	3.0	3.0	3.1	2.5
W						3.6*
X						1.5
X1						0.9
Y						1.4
Z						1.6
g						2.9
g1						1.5
h						1.0
p						0.2

C. tuberculosa Dalman, 1827

	RM Ar27976 Djupvik	RM Ar27977 Djupvik	RM Ar27978 Djupvik	RM Ar27979 Djupvik	RM Ar27980 Djupvik	RM Ar27981 Djupvik
A	5.2	5.6	5.5	5.1	4.9	5.0
B	4.8	5.2	5.0	4.7	4.6	4.6
B1	3.8	4.0	3.8	3.6	3.5	3.5
B3		1.3	1.1	1.1	1.2	1.1
B4		1.4	1.4	1.3	1.3	1.3
C		2.0	2.1		1.8	1.9
D	0.4	0.4	0.5	0.4	0.3	0.4
I	10.4d	11.5	11.3		9.8	
J		5.0	4.9	4.4	4.3	
J1		7.6	7.4	6.5	6.5	6.7
K	3.9	4.3	4.1	3.7	3.7	3.7
K1	3.9	4.3	4.2	3.8	3.7	3.8
K2	3.4	3.9	3.8	3.6	3.4	3.4
K3	2.8	3.3	3.1	2.9	2.8	2.8
K5	2.7*	3.3	3.0	2.8	2.6	2.7
g			3.8	3.5		
g1			2.6	2.1		
h			1.5	1.2		
p			0.4	0.3		

C. tuberculosa Dalman, 1827

	RM Ar27982 Djupvik	RM Ar27983 Djupvik	RM Ar27984 Djupvik	RM Ar28351 Djupvik	RM Ar28349 Djupvik	RM Ar28335 Djupvik
A	5.2	4.7		6.9	7.2	6.5
B	4.8	4.4	3.9	6.3	6.5	6.0
B1	3.6	3.4	3.0	4.8	5.0	4.6
B3	1.2		1.0	1.4	1.6	1.5
B4	1.3		1.1	1.7	1.8	1.7
C	2.0			2.4	2.7	2.4
D	0.4	0.3		0.6	0.7	0.5
I			8.6	13.6d	16.1	
J				6.3	7.5	5.5
J1			6.0*	8.7*	9.5	8.2
K	3.9		3.2	5.0	5.5	4.9
K1	3.9	3.5	3.3	5.0	5.4	4.9
K2	3.5	3.2	2.9	4.8	4.7	4.6
K3	2.9	2.8	2.5	3.8	4.0	3.6
K5	2.8	2.6*	2.4	3.6	4.0	3.6
g				5.1		4.8
g1				2.8		2.3
h				1.8		1.5
p				0.6		0.5

C. tuberculosa Dalman, 1827

	RM Ar28336 Djupvik	RM Ar28350 Djupvik	RM Ar28338 Djupvik	RM Ar28339 Djupvik	RM Ar28340 Djupvik	RM Ar28341 Djupvik
A	5.8	5.6	6.3	6.5	5.9	7.0
B	5.4	5.2	5.9	6.1	5.4	6.5
B1	4.1	3.9	4.5	4.7	4.1	5.0
B3	1.3	1.2	1.4		1.2	1.5
B4	1.4	1.4	1.6		1.4	1.8
C	2.2	2.0	2.4	2.4		2.5
D	0.4	0.4	0.4	0.4	0.5	0.5
I	12.0*	11.6d	13.6		12.1	13.8d
J	5.4	5.3	5.5		5.0	6.2
J1	7.8	7.9	8.8		7.4	9.1
K	4.4	4.4	4.9	4.8	4.3	5.0
K1	4.4	4.3	4.9	4.7	4.3	5.1
K2	4.0	4.0	4.4	4.5	3.9	4.5
K3	3.3	3.4	3.6	3.7	3.2	3.8
K5	3.2	3.3	3.4	3.6	3.1	3.6
g	4.5				4.2	5.1
g1	2.2				2.2	2.6
h	1.3				1.4	1.8
p	0.4				0.4	0.6

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	RM Ar28342 Djupvik	RM Ar28343 Djupvik	RM Ar28344 Djupvik	RM Ar28345 Djupvik	RM Ar28346 Djupvik	RM Ar28347 Djupvik
A	7.4	5.3	5.3	5.9	5.7	5.7
B	6.9	5.0	4.9	5.5	5.3	5.4
B1	5.2	3.9	3.7	4.3	4.0	4.2
B3	1.4	1.1	1.3	1.3	1.2	
B4	1.9	1.4	1.4	1.5	1.4	
C	3.0	2.2	2.0	2.3	2.0	2.1
D	0.5	0.3	0.4	0.4	0.4	0.3
I	15.8	11.0	11.1	12.1		12.2*
J	6.7	4.9	4.6*	5.1*	5.0	5.1
J1	10.2	7.3		7.8	6.9	
K	5.6	4.2	4.1	4.3	3.9	4.5
K1	5.6	4.3	4.0	4.3	3.9	4.5
K2	5.2	3.8	3.8	4.1	3.5	4.1
K3	4.2	3.2	3.0	3.2	2.9	3.3
K5	4.1	3.1	2.9	3.1	2.8	3.2
g	5.3	4.0				4.0
g1	2.5	2.1				2.0
h	1.9	1.4				1.3
p	0.6	0.3				0.4

C. tuberculosa Dalman, 1827

	RM Ar28348 Djupvik	RM Ar28334 Djupvik	RM Ar28337 Djupvik	RM Ar28333 Djupvik	RM Ar28352 Djupvik	RM Ar28353 Djupvik
A	5.6			12.0*	4.9	5.0
B	5.2			11.1*	4.6	4.6
B1	4.0			8.5*	3.6	3.4
B3	1.3			2.8*	1.1	1.2
B4	1.5			3.2	1.3	1.3
C	2.1			4.7*	1.9	2.0
D	0.4			0.9*	0.3	0.4
I	12.1			25.7*	10.4	11.0
J	4.9			12.0d	4.6	4.7
J1	7.6			17.0d	6.9	7.1
K	4.4			9.6	3.9	4.0
K1	4.3			9.4	3.9	4.0
K2	3.8			8.3	3.7	3.6
K3	3.1			6.6	3.1	3.0
K5	3.1			6.4	3.0	2.8
W		9.8	9.4*		4.5	
X		4.7	4.5		2.1	
X1		2.5	2.4			
Y		4.6	4.3			
Z		5.0	4.5		1.9	
g	3.8					3.9
g1	2.0					1.9
h	1.5					1.4
p	0.4					0.4

C. tuberculosa Dalman, 1827

	RM Ar28354 Djupvik	RM Ar28355 Djupvik	RM Ar28356 Djupvik	RM Ar28357 Djupvik	RM Ar28358 Djupvik	RM Ar28359 Djupvik
A	6.2	5.0	5.6	5.3	5.0	5.3
B	5.8	4.6	5.2	4.9	4.7	5.0
B1	4.6	3.6	4.0	3.7	3.6	3.9
B3	1.3	1.2	1.2	1.2	1.1	1.2
B4	1.6	1.2	1.4	1.4	1.3	1.3
C	2.2	1.9	2.1	2.0	1.9	1.9
D	0.4	0.4	0.4	0.4	0.3	0.3
I		9.8	12.1*	10.5	10.2	10.3
J	5.6	4.2	4.9	4.6	4.7	4.5
J1	8.0	6.7	7.5*	7.0	6.9	7.0
K	4.6	3.6	4.2	3.9	3.9	3.9
K1	4.6	3.7	4.1	3.9	3.8	3.9
K2	4.3	3.4	3.8	3.5	3.5	3.6
K3	3.5	2.9	3.1	2.9	2.9	3.1
K5	3.3	2.7	3.0	2.8	2.8	2.9
g		3.4	3.9	3.6		3.6
g1		1.7	2.1	1.8		1.9
h		1.3	1.3	1.4		1.2
p		0.4	0.5	0.4		0.3

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	RM Ar28360 Djupvik	RM Ar28361 Djupvik	RM Ar28362 Djupvik	RM Ar28363 Djupvik	RM Ar28364 Djupvik	RM Ar28365 Djupvik
A	4.0	6.3	5.5	5.4	8.1	3.9
B	3.8	5.8	5.1	5.0	7.6	3.7
B1	3.0	4.4	3.9	3.7	5.9	2.9
B3	0.9	1.6	1.3	1.2		1.1
B4	1.1	1.4	1.5	1.4	2.2	1.0
C	1.5	2.4	2.1	1.9		1.5
D	0.2	0.5	0.4	0.4	0.5	0.2
I	8.1	12.7	11.8	10.8		8.1
J	3.6	5.2	4.8	4.8		3.1
J1	5.6	8.3	7.4	7.0		5.6
K	3.1	4.6	4.4	4.0		3.0
K1	3.1	4.6	4.3	4.1	6.4	3.0
K2	2.8	4.2	3.7	3.7	5.7	2.8
K3	2.4	3.5	3.2	3.1	4.7	2.3
K5	2.3	3.4	3.1	2.9	4.4	2.2
W		5.4				
X		2.5				
X1		1.3				
Y		2.3				
Z		2.5				
g	2.8	4.2	3.7	3.9		3.1
g1	1.5	2.2	2.0	1.9		1.4
h	0.9	1.7	1.3	1.3		1.0
p	0.3	0.6	0.4	0.4		0.3

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	RM Ar28366 Djupvik	RM Ar28367 Djupvik	RM Ar28368 Djupvik	RM Ar28369 Djupvik	RM Ar28370 Djupvik	RM Ar28371 Djupvik
A	5.5	5.2	4.8	5.3	4.7	4.2
B	5.1	4.8	4.5	5.0	4.3	3.9
B1	3.7	3.8	3.5	3.7	3.4	3.0
B3	1.3	1.2	1.2		1.1	1.0
B4	1.4	1.4	1.3		1.2	1.1
C	2.1	1.8	1.8	2.0	1.7	1.5
D	0.4	0.4	0.3	0.3	0.4	0.2
I	11.8	10.8	9.8		9.4	8.3
J	5.3	4.7	4.4		4.2	3.7
J1	7.4	6.9	6.5		6.2	5.6
K	4.2	4.1	3.7	3.7	3.5	3.0
K1	4.1	3.9	3.7	3.8	3.4	3.1
K2	3.9	3.8	3.4	3.7	3.1	2.8
K3	3.2	3.0	2.8	3.0	2.6	2.5
K5	3.2	2.9	2.6	2.9	2.5	2.4
g		3.8	3.6			3.1
g1		2.1	1.8			1.4
h		1.0	1.2			1.0
p		0.3	0.4			0.2

<u>C.</u> <u>tuberculosa</u> Dalman, 1827

	RM Ar28372 Djupvik	RM Ar28373 Djupvik	RM Ar28374 Djupvik	RM Ar28375 Djupvik	RM Ar28376 Djupvik	RM Ar28378 Djupvik
A	5.2*	4.9	5.1	5.3	4.1	4.5
B	4.9*	4.6	4.7	4.9	3.8	4.2
B1	3.8	3.6	3.5	3.7	3.0	3.2
B3			1.1	1.2	1.0	1.1
B4	1.3	1.3	1.3	1.4	1.1	1.2
C	1.9	2.0	1.9	2.0	1.5	1.6
D	0.3	0.3	0.4	0.4	0.5	0.3
I	10.4	10.9*	10.4*	10.9	8.0	9.4
J	4.7	4.5	4.6	4.9	3.6	4.2
J1	6.9	6.8	6.8	6.9	5.5	6.5
K	4.0	4.0	3.8	3.9	3.0	3.5
K1	4.0	3.9	3.8	3.9	3.0	3.5
K2	3.6	3.5	3.4	3.5	2.9	3.3
K3	3.1	2.8	2.8	2.8	2.4	2.7
K5	3.0	2.7	2.6	2.8	2.3	2.6
g	3.8		3.9			
g1	1.9		2.0			
h	1.2		1.2			
p	0.3		0.4			

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	RM Ar28379	RM Ar28380	RM Ar28381	RM Ar28382	RM Ar28383	RM Ar28384
	Djupvik	Djupvik	Djupvik	Djupvik	Djupvik	Djupvik
A	4.8	4.2	4.0	4.5	3.8	3.5
B	4.4	3.9	3.8	4.2	3.6	3.4
B1	3.4	3.2	2.9	3.2	2.9	2.6
B3	1.1	1.1	0.9	1.0	1.0	0.8
B4	1.3	1.1	0.9	1.1	1.0	0.8
C	1.8	1.5	1.4	1.8	1.4	1.2
D	0.4	0.3	0.2	0.3	0.2	0.1
I	10.5	9.1	7.4	9.1	8.1	7.2
J	4.4	4.1	3.5	3.7	3.3	2.9
J1	6.6	5.8	5.1	6.1	5.3	4.9
K	3.8	3.2	2.8	3.3	3.0	2.6
K1	3.8	3.2	2.9	3.4	3.0	2.7
K2	3.5	2.9	2.8	3.1	2.8	2.5
K3	3.0	2.4	2.5	2.5	2.3	2.2
K5	2.9	2.4	2.3	2.3	2.2	2.1
g				3.1	2.8	2.4
g1				1.8	1.5	1.2
h				1.0	1.0	0.8
p				0.3	0.2	0.2

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	RM Ar28385 Djupvik	RM Ar28386 Djupvik	RM Ar28263 Djupvik	RM Ar28264 Djupvik	RM Ar28205 Djupvik	RM Ar28206 Djupvik
A	4.0	3.9	3.4	2.5	3.5	4.0*
B	3.8	3.7	3.2	2.4	3.3	3.8*
B1	2.9	2.8	2.4	1.9	2.5	3.0
B3	1.0	1.0	0.8	0.6	0.8	0.9
B4	0.9	0.9	0.9	0.6	0.9	1.1
C	1.5	1.3	1.2	0.9	1.2	1.4
D	0.2	0.2	0.2	0.1	0.2	0.2
I	7.6	8.0	6.7	4.4*	7.1	8.2
J	3.4	3.5	3.0	1.9	2.9	3.5
J1	5.3	5.4	4.6	3.2	4.8	5.5
K	2.9	3.0	2.5	1.6	2.5	3.1
K1	2.9	3.0	2.6	1.7	2.6	3.1
K2	2.6	2.7	2.4	1.5	2.4	3.0
K3	2.2	2.3	2.1	1.4	2.0	2.4*
K5	2.1	2.2	2.0	1.3	1.9	2.4
g			2.5			
g1			1.2			
h			0.8			
p			0.2			

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	RM Ar28207 Djupvik	RM Ar28208 Djupvik	RM Ar28209 Djupvik	RM Ar28210 Djupvik	RM Ar28211 Djupvik	RM Ar28212 Djupvik
A	3.3	3.8	3.7	4.0	3.7	4.3
B	3.1	3.5	3.4	3.8	3.5	4.0
B1	2.4	2.7	2.7	2.9	2.7	3.1
B3	0.8	0.9	0.9		0.9	1.0
B4	0.9	1.0	0.9	1.0	1.0	1.1
C	1.2	1.4	1.4	1.4	1.3	1.6
D	0.2	0.2	0.2	0.2	0.2	0.3
I	6.5	7.6	6.6*	7.8	7.0	8.7
J	2.7	3.3*	2.9		3.1	3.8
J1	4.5	5.1*	4.9		5.0	5.4
K	2.5	2.6	2.5	2.9	2.7	3.1*
K1	2.5	2.7	2.6	2.9	2.8	3.0
K2	2.2	2.7	2.5	2.7	2.5	2.6
K3	1.9	2.3	2.1	2.7	2.2	2.3
K5	1.8	2.2	2.1*	2.2	2.1	2.2

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	RM Ar28213 Djupvik	RM Ar28214 Djupvik	RM Ar28215 Djupvik	RM Ar28216 Djupvik	RM Ar28217 Djupvik	RM Ar28218 Djupvik
A	3.8	3.6	3.4	3.5	3.4	3.7
B	3.5	3.4	3.2	3.3	3.2	3.5
B1	2.7	2.7	2.4	2.6	2.5	2.7
B3	0.9		0.8	0.8	0.8	0.9
B4	1.0		0.8	0.9	0.9	0.9
C	1.4	1.4	1.2	1.3	1.3	
D	0.2	0.2	0.2	0.2	0.2	0.2
I	7.2	6.1*	6.9	6.9	6.9	7.0*
J		2.8	2.6*	3.0	2.9	2.9
J1	4.9	4.3	4.5	4.6	4.8	4.9
K	2.7	2.4	2.5	2.6	2.5	2.8
K1	2.8	2.4	2.5	2.6	2.5	2.8
K2	2.6	2.2	2.4	2.3	2.4	2.5
K3	2.1	2.0	1.9	2.0	1.9	2.1
K5	2.1	1.9	1.8	2.0	1.9	2.0

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	RM Ar28219 Djupvik	RM Ar28220 Djupvik	RM Ar28221 Djupvik	RM Ar28222 Djupvik	RM Ar28223 Djupvik	RM Ar28224 Djupvik
A	3.5	4.0	3.5	3.5		3.5*
B	3.3	3.7	3.3	3.3	3.5	3.3*
B1	2.5	2.7	2.5	2.6	2.7	2.4
B3	0.9	1.0	0.9	0.9		
B4	0.9	1.0	0.9	0.9	1.0	0.9
C	1.2	1.4	1.3	1.2	1.3	1.2
D	0.2	0.3	0.2	0.2		0.2
I	5.9*		7.1	6.6	6.9*	6.7
J	2.8	3.3	3.2			2.9
J1	4.5	5.2	4.6	4.6		
K	2.4	2.8	2.6	2.5	2.7	2.5
K1	2.4	2.8	2.6	2.6	2.8	2.6
K2	2.2	2.5	2.3	2.3	2.6	2.4
K3	1.9	2.2	2.0	2.1	2.2	2.0
K5	1.8	2.1	1.9	2.0	2.1	1.9
g			2.7			
g1			1.4			
h			0.7			
p			0.2			

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	RM Ar28225 Djupvik	RM Ar28226 Djupvik	RM Ar28227 Djupvik	RM Ar28228 Djupvik	RM Ar28229 Djupvik	RM Ar28230 Djupvik
A	3.4	3.7	3.6	3.5	3.3	3.5
B	3.1	3.5	3.3	3.3	3.2	3.3
B1	2.4	2.8	2.5	2.6	2.4	2.5
B3	0.8	0.9	0.8	0.8	0.8	0.8
B4	0.8	1.0		0.9	0.9	0.8
C	1.2	1.3	1.4	1.3	1.2	1.3
D	0.2	0.2	0.2	0.1	0.1	0.2
I	6.8	7.5	6.6*	6.8	6.6	
J	2.9	3.4	2.7			3.1
J1	4.4	5.2	4.7	4.8	4.6	4.5
K	2.4	2.8	2.5	2.6	2.4	2.6
K1	2.4	2.9	2.5	2.7	2.4	2.6
K2	2.2	2.7	2.2	2.5	2.2	2.3
K3	2.0	2.3	1.9	2.2	1.9	2.1
K5	1.9	2.2	1.8	2.1	1.9	2.0
g			2.3			
g1			1.2			
h			0.7			
p			0.2			

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	RM Ar28231 Djupvik	RM Ar28232 Djupvik	RM Ar28233 Djupvik	RM Ar28234 Djupvik	RM Ar28235 Djupvik	RM Ar28243 Djupvik
A	3.5	3.5	3.5		3.7	3.6
B	3.3	3.3	3.3	3.3	3.5	3.4
B1	2.5	2.4	2.5	2.5	2.7	2.6
B3	0.8	0.8	0.8		0.8	0.9
B4	0.8	0.9	0.9		0.9	0.9
C		1.2	1.3		1.3	1.3
D	0.2	0.2	0.2		0.2	0.2
I	6.7	6.6	6.9	6.6	7.1	6.7*
J		2.7	3.0		3.0	2.9
J1	4.6	4.5	4.5		4.9	4.5
K	2.4	2.5	2.5	2.6	2.6	2.4
K1	2.5	2.6	2.6	2.6	2.7	2.5
K2	2.3	2.2	2.3	2.3	2.4	2.3
K3	2.1	1.9	2.0	2.0	2.1	2.1
K5	2.0	1.8	1.9	1.9	2.0	2.0
g		2.3	2.6			2.3
g1		1.2	1.4			1.2
h		0.7	0.7			0.7
p		0.2	0.2			0.2

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	RM Ar28244 Djupvik	RM Ar28245 Djupvik	RM Ar28246 Djupvik	RM Ar28247 Djupvik	RM Ar28248 Djupvik	RM Ar2824[illegible] Djupvik
A	3.5	3.5	3.4	4.0	3.0	3.0
B	3.2	3.2	3.2	3.7	2.9	2.8
B1	2.5	2.4	2.5	2.9	2.2	2.2
B3	0.8	0.9	0.8			0.7
B4	0.9	0.9	0.9		0.8	0.8
C	1.2	1.3	1.2		1.1	
D	0.2	0.2	0.2	0.3	0.1	0.1
I		6.3			5.8	5.6
J	2.9	2.7	2.6		2.7	
J1	4.8	4.5	4.6		4.1	3.8
K	2.5	2.5	2.4		2.3	2.1
K1	2.6	2.5	2.5	2.5	2.3	2.2
K2	2.3	2.3	2.3	2.3	2.1	2.0
K3	2.0	1.9	2.0	2.0	1.8	1.3
K5	1.9	1.9	1.9	1.9	1.7	1.2
g		2.4			2.0	
g1		1.3			0.9	
h		0.7			0.6	
p		0.2			0.2	

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	RM Ar28243 Djupvik	RM Ar28244 Djupvik	RM Ar28245 Djupvik	RM Ar28246 Djupvik	RM Ar28247 Djupvik	RM Ar28248 Djupvik
A	3.3	3.3	3.3	2.9	3.1	3.2
B	3.1	3.1	3.1	2,7	3.0	3.0
B1	2.4	2.4	2.4	2.1	2.3	2.3
B3	0.8	0.8	0.8	0.7	0.8	
B4	0.8	0.8	0.8	0.8	0.8	0.8
C	1.2	1.2	1.2	1.0	1.2	1.1
D	0.1	0.2	0.2	0.1	0.1	0.2
I	6.5	6.7	6.5	6.1	6.0	6.0
J	2.8	2.7	2.9	2.6	2.6	
J1	4.6	4.3	4.3	4.1	4.3	4.2
K	2.4	2.4	2.4	2.1	2.2	2.3
K1	2.4	2.4	2.4	2.2	2.3	2.3
K2	2.2	2.2	2.2	2.0	2.1	2.1
K3	2.0	1.9	1.9	1.8	1.8	1.9
K5	1.9	1.8	1.9	1.7	1.8	1.8

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	RM Ar28249 Djupvik	RM Ar28236 Djupvik	RM Ar28237 Djupvik	RM Ar28238 Djupvik	RM Ar28239 Djupvik	RM Ar28240 Djupvik
A	3.1	3.1	2.6	2.5	2.6	2.7*
B	2.9	2.9	2.5	2.4	2.4	2.5*
B1	2.3	2.2	1.9	1.8	1.8	2.0
B3	0.8	0.9	0.7	0.6	0.6	
B4	0.8	0.8	0.7	0.6	0.7	0.8
C	1.1	1.2	1.0	1.0*		1.1
D	0.1	0.1	0.1	0.1	0.1	0.1
I	6.3	6.3	5.2	5.0*	5.0	5.3*
J	2.5		2.2	2.1		2.3
J1	4.0	4.6	3.7	3.5	3.6	3.6
K	2.2	2.4	1.9	1.8	1.8	2.0
K1	2.3	2.4	1.9	1.9	1.9	2.0
K2	2.1	2.1	1.7	1.6	1.6	1.8
K3	1.8	1.9	1.5	1.5	1.5	1.6
K5	1.7	1.8	1.4	1.4	1.4	1.5

C. tuberculosa Dalman, 1827

	RM Ar28241 Djupvik	RM Ar28242 Djupvik	RM Ar28243 Djupvik	RM Ar6230 Djupvik	SM A84000 Wenlock Edge	SM A84001 Wenlock Edge
A	3.1	3.2	3.4	9.4	11.1	13.4
B	3.0	3.0	3.2	8.6	10.2	12.3
B1	2.3	2.4	2.4	6.5	7.6	9.4
B3	0.8	0.8	0.9	1.7	3.0	3.8
B4	0.8	0.8	0.9	2.3	2.8	3.2
C	1.1	1.1	1.2	3.6	4.0	5.2
D	0.1	0.1	0.2	0.8	0.9	1.1
I	6.0*	6.5	6.5	20.0	23.2d	
J	2.5	2.8	2.8	8.9	7.8	
J1	4.2	4.5	4.5	12.6	14.5	
K	2.2	2.5	2.4	7.4	9.0	
K1	2.2	2.5	2.4	7.2	9.0	10.4
K2	1.9	2.3	2.2	6.4	8.1	9.0
K3	1.7	1.9	1.9	5.1	6.5	
K5	1.7	1.9	1.8	5.0	6.3	
g				7.2*		
g1				3.2		
h				2.5		
p				0.8		

C. tuberculosa Dalman, 1827

	RM Ar47851 Djupvik	RM Ar28441 Djupvik	RM Ar28442 Djupvik	RM Ar28443 Djupvik	SM A84003 Wenlock Edge	SM A84004 Wenlock Edge
A	14.9					
B	14.0					
B1	10.7					
D	0.9					
K1	12.6					
K2	11.5					
K3	9.6*					
K5	9.2*					
W					4.5	9.5
X					2.2	5.0
X1					1.3	2.2
Y					2.2	4.8
Z					2.5	5.2
a	6.5	3.4	4.2	3.3		
b	7.3*	4.2	5.1	4.0		
b1	4.8	2.5	3.2			
b2	4.7	2.6	3.0*	2.2		
b3	3.0	1.8	2.0*	1.6		
d	9.0	4.6	5.8*	4.4*		
e	5.6	3.2	4.0	2.8*		
e1		2.0	1.8	1.6		
e2	0.8	0.4	0.5			

C. neointermedia R. & E. Richter, 1954

	RM Ar47730 Gotland	RM Ar47718 Gotland	RM Ar47724 Gotland	RM Ar47716 Gotland	RM Ar47727 Gotland	RM Ar47717 Gotland
A	8.0				11.4*	
B	6.2	8.5			8.6*	6.9
B1	4.7	6.8			6.7*	5.4
B2	1.2	1.6				
B3	2.2	2.4		2.4	2.4*	2.0
B4	1.7	2.4			2.4	1.9
C	2.3	3.5		3.2	3.8*	
D	1.8			2.4	2.6	
I	15.8d	22.2d		21.2		19.4d
J	6.9			9.1	9.3	8.0*
J1	8.6	11.7		11.5		9.6
J2	7.6			10.2		9.0
K	4.8	6.8	7.8		7.5	5.7
K1	4.9	7.0	7.9	6.4	7.4	5.8
K2	4.6	6.2		5.9	6.4	5.4
K3	4.0	5.0		4.9	5.3	4.4
K5	3.8	4.8		4.8	5.2	4.3
W	6.0			8.4		7.1
X	2.8			3.5		3.2
X1	1.9			2.0		1.8
Y	2.5					2.6
Z	2.8			3.1*		3.0

<u>C. neointermedia</u> R. & E. Richter, 1954

	RM Ar6225 Petesvik	RM Ar47722 Gotland	RM Ar47714 Gotland	RM Ar47741 Gotland	RM Ar47733 Gotland	RM Ar47715 Gotland
A	10.8	8.8*	12.4*	6.6	8.4*	
B	8.4	6.7*	9.6*	5.3	6.8	6.8*
B1	6.5	5.3	7.6	4.1	5.3	5.2
B3	2.5		2.7	1.6	1.8	1.9
B4	2.4		2.7	1.5	1.9	1.9
C	3.5		4.2	2.1	2.7	2.9
D	2.4	2.1	2.8	1.3	1.8	
I			27.0d	10.8d	15.9d	17.4d
J	9.6	7.8*	10.5	6.0	7.2	
J1	12.2d	9.5	14.3	7.7	9.3d	9.8d
J2	10.4d	8.4	12.4*	7.0	8.4	8.8d
K	6.5*	5.2	8.2	4.3	5.4	5.6
K1	6.7*	5.4	8.1	4.4	5.7	5.7
K2	6.2d	5.0	7.4	4.3	5.2	5.0
K3		4.3	6.1	3.6	4.3	4.3
K4			5.8			
K5	5.3	4.2	5.6	3.5	4.0	4.0
W		7.1		5.3	7.2	6.9
X		3.1		2.4	3.1	3.2
X1		1.7		1.3	1.7	1.8
Y		2.9		1.9	3.0	2.9
Z		3.2		2.1	3.4	3.2

C. neointermedia R. & E. Richter, 1954

	RM Ar47728 Gotland	RM Ar47736 Gotland	RM Ar47737 Gotland	RM Ar47734 Gotland	RM Ar47739 Gotland	RM Ar47735 Gotland
A	7.5	8.0	6.4	7.9	6.3	
B	6.0	6.4	5.2	6.4	5.1	
B1	4.7	5.1	4.0	5.0	3.8	
B3		1.7	1.4	1.9	1.5	
B4	1.6	1.6	1.4	1.7	1.4	
C		2.5	2.2	2.4	1.9	
D	1.5	1.6	1.2	1.5	1.2	
I					12.2	14.2
J	6.5		5.6	7.2	5.4	
J1				8.5	7.1	8.8
J2			6.4	7.6	6.4	
K	4.6	4.9	4.1	4.7	4.0	
K1	4.8	5.1	4.2	5.1	4.2	4.9
K2	4.6	4.8	3.8	4.7	3.9	4.6
K3	3.8	4.1*	3.3	3.9	3.3	
K5	3.7	4.0*	3.2	3.8	3.2	
W	6.0	5.8*	4.8	5.9		
X	2.6	2.8	2.3	2.7		
X1	1.5	1.7	1.3	1.9		
Y	2.3	2.2	1.9	2.5		
Z	2.5	2.4	2.1	2.8		

C. neointermedia R. & E. Richter, 1954

	RM Ar47729 Gotland	RM Ar47720 Gotland	RM Ar47725 Gotland	RM Ar47721 Gotland	RM Ar47723 Gotland	RM Ar47739 Gotland
A	9.7	8.2		10.1		8.2
B	7.4	6.5		7.8		6.4
B1	5.6	5.0		5.9	6.2	4.9
B3		1.9				2.0
B4		1.8			2.2	1.8
C		2.4	3.4	3.0		2.6
D	2.3	1.7		2.3	2.2*	1.8
I	19.2			21.2d	21.1	
J	8.4	7.1		9.2	9.3	7.4d
J1		9.4		12.2d		9.6
J2		8.2		10.3		8.5
K	6.2	5.1	6.4	6.5		5.5
K1	6.4	5.2	6.5	6.5	6.6	5.4
K2	5.3	4.8	5.9	6.0	6.1	5.0
K3	4.4	4.0		4.8	5.0	4.1
K5	4.3	3.9		4.5	4.8	3.8
W	7.8	6.2		8.7	9.0	7.1
X	3.4	3.0		3.8*	4.0	3.0
X1	1.9	1.7			2.4*	1.7
Y	3.2	2.5		3.9		2.5
Z	3.5	2.7		4.4	4.6	2.9

_C_. _neointermedia_ R. & E. Richter, 1954

	RM Ar47738 Gotland	RM Ar47740 Gotland	RM Ar47726 Gotland	RM Ar47754 Gotland	RM Ar47753 Gotland
A	5.1	5.2		6.0	
B	4.1	4.2	6.0	4.9	
B1	3.2	3.3	4.7	3.9	4.7
B3	1.3	1.3		1.4	1.9
B4	1.0	1.1		1.2	1.6
C	1.5	1.5	2.5	1.9	2.4
D	1.0	1.0		1.1	1.8
I	9.2d	9.6	15.4d		15.4
J	4.3	4.5		5.1	6.5
J1	5.5	5.8		6.5	7.3
J2	5.0	5.3		5.9	8.4
K	3.2	3.1	5.0	3.6	
K1	3.3	3.2	5.2	3.8	4.9
K2	2.9	2.8	4.8	3.7	4.5
K3	2.5	2.6	3.8	3.1	3.7
K5	2.4	2.5	3.6	3.0	3.6
W	3.7	3.8	6.2		6.0
X	1.7	1.7	2.6		2.9
X1		1.0	1.6		
Y1			2.1*		
Z	1.7	1.6	2.3		2.5

<u>C.</u> <u>neointermedia</u> R. & E. Richter, 1954

	RM Ar47742 Gotland	RM Ar47747 Gotland	RM Ar47746 Gotland	RM Ar47744 Gotland	RM Ar47750 Gotland	RM Ar47749 Gotland
A	6.9	6.6				8.2
B	5.6	5.4	4.7		8.4	6.5
B1	4.3	4.3	3.7		6.5	5.1
B3	1.6	1.5	1.3		2.3	
B4	1.5	1.5	1.2		2.3	
C	2.1	1.9	1.3		3.5	2.6
D	1.3	1.2				1.7
J	6.1	6.2				7.2
J1		7.4			12.2	9.1
J2	7.2	6.8			10.7	8.3
K	4.1	4.3	3.6		6.5	5.3
K1	4.2	4.4	3.8	5.1	6.6	5.4
K2	4.0	4.2	3.5		6.1	5.0
K3	3.2	3.5	2.9		5.3	4.3
K5	3.2	3.3	2.8		5.0	4.2
W	5.0	5.3	4.5		8.8	6.8
X	2.5	2.3	1.9		4.0	3.2
X1	1.5	1.4	1.2		2.2	1.9
Y	2.2		1.7		3.7	2.8
Z	2.4		1.9		4.2	3.1

C. neointermedia R.& E. Richter, 1954

	RM Ar47751 Gotland	RM Ar47745 Gotland	RM Ar47743 Gotland	RM Ar47755 Gotland	RM Ar47756 Gotland	RM Ar47748 Gotland
A	8.6		6.8	5.0	9.3*	7.8
B	6.8*		5.3	4.2	7.2*	6.2
B1	5.1		4.1	3.3	5.5*	6.5*
B3	2.0	2.1	1.6	1.3	2.2	
B4	2.0	1.9	1.5	1.1	2.1	1.4
C	2.5	2.6	2.2	1.6	2.9	
D	1.8		1.5	0.8*	2.1	1.6
I	18.1	17.8		10.6		16.8d
J	8.0		5.4	4.6	8.4	7.3
J1	10.0		7.4	5.9		
J2	9.0		6.7	5.3	9.4d	8.3
K		5.5	4.2	3.2		5.2
K1	5.8	5.7	4.3	3.4	5.9	5.4
K2	5.2	5.0	4.1	3.1	5.3	4.8
K3	4.3	4.2	3.5	2.9	4.4*	4.1
K5	4.2	4.2	3.4	2.7	4.2*	4.0
W	7.0	7.0	5.4	4.1	7.5	
X	3.1		2.4	1.8	3.5	
X1			1.4		2.0	
Y			2.0	1.4	3.4	
Z	2.7		2.2	1.5	3.8	

C. neointermedia R. & E. Richter, 1954

	RM Ar47750 Gotland	RM Ar6228 Petesvik	RM Ar27163 Petesvik	RM Ar47789 Petesvik	RM Ar47790 Petesvik	RM Ar47791 Petesvik
A	6.2	14.0	11.8		5.5	4.6*
B	5.0	10.8	9.3	3.1	4.6	3.9
B1	3.9	8.3	7.2	2.4	3.6	3.0
B3	1.3	2.6	2.5		1.2	1.1
B4	1.3	2.8	2.5*		1.2	1.0
C	1.8	4.2	3.9	1.1	1.7	1.5
D	1.2	3.2	2.5		0.9	0.8*
I	11.6d			6.2d		8.8d
J	5.3	12.8		2.9		
J1	6.8	15.3	13.8			5.5
J2	5.8	13.9	12.1	3.6		5.0*
K	3.8	8.3	7.4	2.3		3.0
K1	4.0	8.6	7.6	2.4		3.2
K2	3.6	7.9	7.0	2.2		3.2
K3	2.9	6.2	5.7	1.9		
K4						2.7
K5	2.8	6.2	5.5	1.8		2.5
W		10.9	10.3			
X		5.0	4.5			
X1			2.5			

C. neointermedia R. & E. Richter, 1954

	RM Ar47840 Hablingbo	RM Ar47841 Hablingbo	RM Ar47842 Hablingbo	RM Ar47843 Hablingbo	RM Ar27079 Petesvik	RM Ar27080 Petesvik
A	4.9*		3.8	6.3*	10.6	4.4
B	3.9	4.1*	3.2	5.1	8.1	3.7
B1	3.1	3.2*	2.5	3.0	6.2	2.9
B3	1.2		0.8		2.6	1.2
B4	1.1		1.0		2.3	1.0
C	1.5	1.7*	1.2		3.4	1.4
D	0.9		0.6	1.2*	2.5	0.6
I	9.2d		7.0d		22.1	
J	4.3*		3.9	5.4	9.6	
J1	5.6				12.0	
J2	4.9				10.9	
K	3.0*	3.5	2.3	3.9	6.5	2.9
K1	3.2	3.6	2.5	4.1	6.9	3.1
K2	3.0	3.4	2.3	3.8	6.3	2.8
K3		2.9	2.0	3.3	5.2	2.4
K4	2.5					
K5	2.4	2.7	2.0	3.2	4.9	2.3
W		4.1				
X		1.9				
X1		1.2				
Y		1.9				
Z		2.0				

C. neointermedia R. & E. Richter, 1954

	RM Ar27081 Petesvik	RM Ar27082 Petesvik	RM Ar27083 Petesvik	RM Ar47796 Petesvik	RM Ar47797 Petesvik	RM Ar27141 Petesvik
A	7.0	6.8	7.1	10.2	9.2	
B	5.5	5.4	5.6	8.2	7.3	
B1	4.3	4.3	4.4	6.4	5.7	
B3	1.7		1.7*	2.4	2.2	
B4	1.6	1.5	1.5	2.4	1.9	
C	2.2	2.2	2.2	3.2	2.9	
D	1.5	1.4	1.5	2.0	1.9	
I	15.2d				17.0d	
J	6.7	6.1	6.5	9.2d	8.5	
J1	8.2d		8.1d	11.3	10.1d	
J2	7.6d		7.2d	10.5	9.0d	
K	4.6	4.3	4.5	6.5	5.7	
K1	4.7	4.4	4.8	6.8	5.9	
K2	4.2	4.0	4.2	6.3	5.5	7.5
K3	3.8	3.5	3.7	5.2	4.6	
K5	3.6	3.4	3.6	4.9	4.5	
W	5.7					
X	2.5					
X1	1.5*					
Y	2.4					
Z	2.7					

C. neointermedia R. & E. Richter, 1954

	RM Ar27142 Petesvik	RM Ar27143 Petesvik	RM Ar27144 Petesvik	RM Ar27145 Petesvik	RM Ar27146 Petesvik	RM Ar27147 Petesvik
A	7.5	8.0*	8.6	7.9	7.5	4.5
B	6.0	6.5	6.5	6.3	6.0	3.8
B1	4.8	5.1	5.0	5.0	4.7	2.9
B3	1.8	1.9	2.0		1.8	1.1
B4	1.6	1.7	1.8		1.7	1.0
C	2.3	2.5	2.5		2.3	1.5
D	1.5	1.5*	2.1	1.6	1.5	0.7
I	14.9	16.9d				8.9
J	6.8*		7.7	6.5	6.5	4.0
J1	8.3		9.5		8.8	5.3
J2	7.7		8.3		7.6	4.9
K	4.7	5.1	5.4	4.7	4.9	2.9
K1	4.9	5.4	5.4	5.1	5.1	3.1
K2	4.3	5.1	4.9	4.5	4.5	2.8
K3	3.8*	4.3*	4.1	3.9	3.9	2.4
K5		4.2*	4.1	3.8	3.8	2.4
W	5.8	6.7	6.6	6.1		3.5
X	2.6	3.1	2.9	2.9		1.5
X1		1.7	1.8	1.7		1.0
Y	2.5	2.8	2.8			
Z	2.7	3.1	3.1	2.6		1.4

C. neointermedia R. & E. Richter, 1954

	RM Ar27148 Petesvik	RM Ar27149 Petesvik	RM Ar47798 Petesvik	RM Ar6219 Petesvik	RM Ar6220 Petesvik	RM Ar6218 Petesvik
A			11.1*	11.3	9.6	10.9
B		5.1*	8.6*	8.7	7.7	8.5
B1		3.9*	6.7	6.7	5.8	6.5
B3		1.5			2.2	2.4
B4		1.4		2.3	2.1	2.3
C	1.4	2.1	3.6*		3.0	3.6
D			2.5	2.6	1.9	2.4
I		12.9		23.4d		
J			10.0	10.0	8.6	9.8
J1		6.8*	12.4		11.2*	
J2		6.1	11.2*		9.3*	11.3*
K		4.1	7.0	7.1	6.3	7.1
K1		4.3	7.0	7.1	6.5	7.1
K2		3.8	6.4	6.6	5.7	6.3
K3		3.3	5.4	5.4*	4.7*	5.1
K5		3.2	5.3	5.3	4.6	4.9
W		5.2		9.3	7.9	
X		2.3		4.0	3.2	
X1		1.5		2.2	2.0	
Y		2.1		3.3		
Z		2.4		3.6	3.0	

C. neointermedia R. & E. Richter, 1954

	RM Ar47792 Petesvik	RM Ar47793 Petesvik	RM Ar27153 Petesvik	RM Ar27154 Petesvik	RM Ar27159 Petesvik	RM Ar27157 Petesvik
A			7.6	8.6		
B	4.3	4.8	6.0	6.9	7.4	
B1	3.3	3.7	4.7	5.4	5.8	
B3	1.4		1.7	2.2		
B4	1.2		1.7	2.0		
C	1.6		2.3			
D			1.6	1.7		
I	10.5					
J			6.4	8.0		
J1	6.2		8.3*	10.1		
J2	5.5		7.6	8.9		
K	3.6	3.6	4.7	5.5	5.9	7.5
K1	3.7	3.8	4.9	5.8	6.2	7.5
K2	3.4	3.6	4.4	5.6	5.5	6.7
K3	2.8	3.0	3.6	4.4	4.7	
K5	2.7	2.9	3.5	4.2	4.5	
W	4.1	4.4			8.0	
X	1.8	2.0			3.5	
X1	1.1	1.3			2.0	
Y	1.7	2.0			3.2	
Z	1.9	2.2			3.4	

C. neointermedia R. & E. Richter, 1954

	RM Ar47800 Petesvik	RM Ar47803 Petesvik	RM Ar47802 Petesvik	RM Ar47801 Petesvik	RM Ar47794 Petesvik	RM Ar47857 Petesvik
A	6.0	8.9	8.3	5.0	9.5	9.4
B	4.7	6.8	6.5	4.1	7.5	7.5
B1	3.6	5.3	5.0	3.2	5.8	6.0
B3	1.6		1.9		2.2	2.3
B4	1.3	1.9				2.2
C	1.9	2.9*	2.1	1.5	3.0	3.0
D	1.3	2.1	1.8	0.9	2.0	1.9
I	12.0d	18.3			18.8d	
J	5.2	8.0	6.6	4.4	8.3	8.0
J1	7.0	10.0d	9.4	5.7	10.5	10.3
J2	6.1	8.8d	7.8	5.1*	8.9	9.0
K	3.8	5.5	5.1	3.1	5.7	5.8
K1	3.9	5.6	5.3	3.3	5.9	5.9
K2	3.5	5.2	4.7	3.1	5.3	5.5
K3	3.0	4.3	4.1	2.7	4.5	4.7
K4					4.4	4.4
K5	2.9	4.2	3.9	2.6	4.3	4.4

C. neointermedia R. & E. Richter, 1954

	RM Ar47856 Petesvik	RM Ar47788 Petesvik	BM 58676 Gotland	BM 46390(1) Gotland	BM 46390(2) Gotland	RM Ar47844 Hablingbo
A	7.1	10.9	10.7	7.9	12.0	
B	5.7	8.4	8.0	6.3	9.3	4.3
B1	4.4	6.6	6.0*	4.9	7.0	3.4
B3		2.3	2.6	1.9	2.9	1.2
B4		2.3	2.3	1.6	2.6	1.1
C		3.3	3.4	2.4	3.6	1.5
D	1.4	2.5	2.7	1.6	2.7	
I			22.8	15.5	25.5	10.2
J	5.8	9.4	10.1	6.7	10.3	
J1	8.2d	11.8d	12.7	8.8	14.0	5.2
J2	6.6	10.2d	10.9	7.5	11.6	
K	4.5	6.8	7.2*	4.9	7.8	
K1	4.7	6.8	7.2*	5.1	8.0	3.6
K2	4.3	6.3	6.5	4.7	6.9	3.4
K3	3.6	5.3	5.4*	3.8	6.0	
K4						2.8
K5	3.5	4.8	5.2	3.5	5.8	2.8
W			8.9	6.0		
X			4.1	2.9	4.6	
X1				1.8	2.4	
Y				2.2		
Z				2.5		

C. neointermedia R. & E. Richter, 1954

	RM Ar27104 Havdem	BM It9145 Malverns	RSM 1967-58.117. Dudley?	RM Ar47731 Gotland		RM Ar47731 (cont.d) Gotland
A	10.0*	7.2*	8.3	8.5	a	3.4
B	8.0*	5.8	6.6	6.8	b	3.8
B1	6.3*	4.5	5.1	5.3	b1	2.6
B3		1.8	2.0	1.9*	b2	2.5
B4		1.6	1.9	1.9	b3	1.5
C	3.1*	2.3	2.8*	2.7	d	4.2
D	2.0*	1.4	1.7	1.7	e	2.9
I		14.3		16.6d	e1	1.5
J	8.4	6.4	8.1	7.6	g	5.9
J1	11.1*	8.3	9.0d	9.6d	g1	2.5
J2	9.6	7.4		8.7d	h	2.1
K		4.6	5.6	5.3	p	0.6
K1		4.7	5.8	5.5		
K2	5.7	4.3	5.2	4.8		
K3	4.7	3.6	4.6	4.2		
K5	4.5	3.5	4.3	4.0		
W		6.0	7.3			
X		2.6	3.2			
X1		1.6	1.4			
Y		2.2				
Z		2.5	2.7*			

C. puellaris Reed, 1920

	RM Ar27103 Havdhem	RM Ar27106 Havdhem	RM Ar27105 Havdhem	RM Ar27161 Rone Kanal	RM Ar27126 Eke	RM Ar27107 Fardhem
A	9.8*			8.7	10.1	6.8
B	7.5*	7.4	4.4*	6.8	7.6	5.1
B1	5.8*	5.8	3.4	5.3	5.9	3.8
B3				1.9	2.0	1.5
B4				1.7	1.9	1.3
C		3.2*		2.8	3.5	1.9
D	2.3			1.9	2.5	1.7
I	22.4	20.2			22.6	14.3d
J	10.0	8.6	5.3	7.6	10.3	5.9
J1		11.7	7.2	10.3	12.8	7.4
J2		10.5	6.4	9.2	11.5	6.6
K		6.0	3.4	5.3	6.1	4.2
K1	6.1	5.9	3.3	5.3	6.1	4.1*
K2	5.5	5.5	3.3	5.0	5.7	3.6
K3	4.6*	4.4	2.7	4.1	4.7	3.1*
K4		4.4		4.0	4.6	
K5	4.5	4.2	2.6	3.8	4.4	2.9
W					11.2	
X					3.5	
X1					2.3	

C. puellaris Reed, 1920

	RM Ar27110 Fardhem	RM Ar27109 Fardhem	RM Ar27139 Vanges Kanal	RM Ar27127 Burs Kanal	RM Ar27128 Burs Kanal	RM Ar27077 Vanges Kanal
A	5.5		10.9	8.4	8.4	7.5
B	4.3		8.8	6.5	6.3	5.7
B1	3.3	5.1*	6.9	4.9	4.9	4.5
B3	1.2			1.8	1.8	1.6
B4				1.7	1.7	1.4
C	1.7			2.8	2.7	2.3*
D	1.2	1.6*	2.1	1.9	2.1	1.8
I	11.5d		24.4	17.6		15.1d
J	5.0	7.1	10.4	8.0	7.0	6.9
J1	6.6			10.8	10.6*	9.6
J2	5.7			9.3	9.2*	8.5
K	3.7		7.3	5.3	5.1	4.5
K1	3.6	5.2	7.0	5.1	5.0	4.4
K2	3.2	4.8	6.2	4.9	4.8	4.3
K3	2.8	4.0	5.5	3.9	3.8	3.5*
K4				3.9	3.7	
K5	2.7	3.7	5.3	3.8	3.6	3.4*
W				8.5		6.7
X				3.2		2.7
Z				3.2		2.3

C. puellaris Reed, 1920

	RM Ar27078 Vanges Kanal	RM Ar27113 Alva Kanal	RM Ar27112 Alva Kanal	RM Ar27114 Alva Kanal	RM Ar27115 Alva Kanal
A	8.2	7.5*	6.8		
B	6.2	5.7*	5.1	4.2	2.8
B1	4.7	4.5*	3.8	3.3	2.2
B3		1.5	1.5	1.3	1.0
B4		1.4	1.3	1.8	0.7
C		2.4	2.2		0.9
D	2.0	1.8	1.7		
I		14.9	13.8	11.3	6.3*
J	7.2	6.7	5.8	5.0	
J1		9.3	8.5		4.1
J2	8.8	8.0	7.2		3.6
K	4.9	4.6	4.0	3.4*	2.0
K1	4.7	4.6	4.0	3.5*	2.0
K2	4.4	4.2	3.7	3.2*	1.9
K3	3.5	3.6*	3.1	2.7*	1.6
K5	3.5	3.4*	2.9	2.6*	1.6*
W				5.1	
Z				2.0	

C. puellaris Reed, 1920

	RM Ar47795 Petesvik?	RM Ar47785 Petesvik ?	RM Ar47786 Petesvik ?	RM Ar27076 Vanges Kanal	RM Ar47787 Petesvik ?	RM Ar32767 Klinta
A	9.0	7.9	7.0	8.4	7.5	9.4
B	7.2	6.1	5.6	6.7	6.0	7.5
B1	5.8	4.6	4.3	5.3	4.6	5.8
B3	1.7			1.8	1.4	2.2
B4	1.7			1.7*	1.5	1.8
C	3.0			2.7	2.6	2.9
D	1.8	1.8	1.4	1.7	1.5	1.9
I	19.4d				16.4	18.7
J	8.5	7.2d	6.2	7.7	7.3	8.3
J1	11.3			10.2	10.0	10.9
J2	10.1		7.6*	9.5	9.1	9.5
K	5.6	4.6*	4.2	5.1	4.9	5.5
K1	5.6	4.6	4.2	5.1	4.8	5.6
K2	5.0	4.2	3.9	4.9	4.4	5.3
K3	4.5	3.6	3.4	4.1*	3.7	4.6
K4	4.3*					4.4
K5	4.2	3.5	3.3	3.9*	3.5	4.2
W				7.6	7.6	
X				3.0	2.9	
Y					2.4	
Z				3.4	2.6	
g				5.0	4.8	
g1				2.5	2.4	
h				1.7	1.2	
p				0.9	1.0	

C. puellaris Reed, 1920

	RM Ar32778 Klinta	RM Ar32773 Klinta	DJS/13 (S) Usk	DJS/20b (C) Usk	DJS/21 (C) Usk	DJS/19 (S) Usk
A	6.7	4.9	8.8		6.9	5.7
B	5.6	4.0	6.4		5.3	4.5
B1	4.4	3.2	5.0	4.1*	4.2	3.6
B3	1.5	1.2	1.9	1.5	1.5	1.1
B4	1.4	1.0	1.6	1.2	1.4	1.0
C	2.0	1.3	2.6			1.6
D	1.1	0.9	2.4	1.6	1.6	1.2
I	14.2d	8.7d	17.7			
J	6.6	4.2	8.8		6.0*	5.7
J1	8.0	5.6	10.4	8.8	6.9*	7.1
J2	7.1	4.9	9.1		6.5*	6.3
K	4.2	2.9	4.5		3.2*	3.3
K1	4.3	3.0	4.6	4.5	3.4*	3.4
K2	4.1	2.9	4.4	4.2	3.1*	3.1
K3	3.5	2.6	3.6	3.5	2.7*	2.7
K5	3.2	2.4	3.5	3.1*	2.7*	2.5*

C. puellaris Reed, 1920

	DJS/17a (S) Usk	DJS/130 (S) Usk	DJS/131a (S) Usk	DJS/132a (S) Usk	DJS/132b (C) Usk	DJS/133 (C) Usk	DJS/134 (C) Usk
A	4.7	6.6	7.0	5.7	6.3	9.4	
B	3.6	5.2	5.1	4.2	4.7	7.0	
B1	2.9	4.1	4.1	3.3	3.7	5.5	4.2
B3	1.0	1.5	1.5*		1.4	2.0	1.8
B4	0.8	1.3	1.2		1.1	1.9	
C	1.1	2.0	1.7	1.7	1.7		
D	1.1	1.4	1.9	1.5	1.6	2.4	1.6
I	8.2		13.7	11.9			
J	4.2	6.2*	6.5*	5.8	6.1	9.2d	7.1
J1	4.6		8.0	7.0*	7.3	11.4d	8.4*
J2	4.4	6.8	6.7		6.6	10.2d	7.5
K		3.6	3.5	3.3	3.4	5.7*	
K1	2.5	3.8	3.6	3.4	3.6	5.8	4.3d
K2	2.3	3.4	3.5	3.2	3.4	5.4	3.7
K3	2.7	2.9	2.8	2.6	2.8	4.4d	3.1
K4	2.1		2.7			4.3d	
K5	1.9	2.7	2.7	2.5	2.7	4.2d	3.0

C. puellaris Reed, 1920

	DJS/135 (S) Usk	DJS/136 (S) Usk	DJS/52 (S) Ludlow	DJS/53 (S) Ludlow	DJS/54 (S) Ludlow	DJS/137 (S) Ludlow	DJS/138 (C) Ludlow
A	5.7	3.0	5.8		3.1		
B	4.3	2.3	4.3	4.0	2.6	4.1	4.1
B1	3.4	1.9	3.4	3.3	2.1*	3.3	3.3
B3			1.4	1.2			
B4			1.1	1.0			
C	1.6		1.7*	1.4*		1.8	
D	1.4	0.7	1.5		0.5		0.9
I	12.2					13.0	
J		2.4*	5.7	6.0		5.9*	3.8
J1	7.0*						
J2	6.3*		6.3*			6.3*	4.1
K	3.1		3.6	3.7			
K1	3.4	1.5	3.7	3.7	1.7*	3.4	
K2	3.1	1.3	3.5	3.4	1.6*	3.2*	2.3
K3	2.5	1.2	2.7	2.9		2.6	2.2
K5	2.4	1.2	2.7	2.9	1.4*	2.6	2.0

C. puellaris Reed, 1920

	BM It5766 (C) Ludlow	BM It577 (S) Ludlow	SM A3319 (S) Ludlow	GSM DEW4640 (S) Usk	M1 (S) Builth	DJS/12a (S) Woolhope
A	4.6	6.2*	4.8*	7.9		8.5
B	3.6	4.8*	3.6*	6.1	4.4*	6.8
B1	2.9	3.8*	3.1	4.9	3.8*	5.4
B3	1.2		1.1	1.7	1.4	
B4	1.1		0.9	1.7	1.1	
C	1.4	2.1*	1.5	2.4	1.9	2.5
D	0.9	1.4*	1.2	1.7	1.4	1.7*
I	10.6d			19.0	11.0	15.8
J	4.7d		4.3	8.6	5.6	7.4
J1	5.8d		5.2	10.3*	6.7	
J2				9.5*	6.0	
K	2.7		2.6	5.2	3.0	4.5
K1	2.9		2.8	5.2	3.2	5.0
K2	2.8		2.7	4.6	3.1	4.2
K3			2.3	3.9		3.8
K5			2.2	3.8	2.6	3.4

C. puellaris Reed, 1920

	SM A36814 (S) May Hill	SM A36815 (S) May Hill	GSM DEW4025 (S) Usk	BU MY36U65 (C) May Hill	BU MY36U67 (C) May Hill	BU MY4N264 (S) May Hill
A		6.7	10.0*	5.8*	5.5	
B		4.8	6.9*	4.3*	4.5	3.4
B1	4.0	3.9	5.5	3.4*	3.5	2.8
B3		1.6		1.3	1.2	1.0*
B4		1.3		1.0	1.0	0.9
C		2.1	3.0*	1.7	1.5	1.4
D	1.7	1.9	3.1*	1.5*	1.1	
I		15.2		12.0d		8.0d
J	6.5*	6.7	10.4d	5.5*		4.1
J1		8.6				
K	4.0	4.1		3.3	3.3	2.4
K1	4.0	4.1		3.4	3.4	2.6
K2	3.6	3.7		3.3	3.3	2.4
K3	3.1			2.7	2.7	2.1
K5	2.9	3.0	3.9	2.6	2.5	2.0

C. puellaris Reed, 1920

	BU MY4N261 (S) May Hill	BU WB105 (S) non loc	GSM 19691 (S) Usk	GSM FGD1205 (S) W Borders	BM no no. (S) Wen. Edge	SM A3320 (S) May Hill
A		4.4		5.3	3.0	
B	4.0	3.5	5.5	3.8	2.3	
B1	3.2	2.8	4.4	2.9	1.9	
B3	1.4	1.1		1.4	0.7	
B4	1.1	0.9	1.3	1.0	0.5	
C		1.4		1.4	0.8	
D		0.9		1.5	0.6	2.5
I	12.0d	9.8d			5.7	14.2
J		4.9			2.7	
J1		2.9			3.4	
J2		6.0			3.1*	
K	3.2	2.9			1.6	
K1	3.2	2.9	4.1	2.9	1.7	
K2	2.8	2.8	3.7	2.6	1.6	
K3	2.5	2.3	3.0	2.2	1.4	
K5	2.2	2.3	2.9	2.0	1.4	

Calymene patustria sp. nov.

	RM Ar47855 Petesvik	RM Ar47797 Petesvik	RM Ar47858 Petesvik	RM Ar27150 Petesvik	RM Ar27151 Petesvik	RM Ar27152 Petesvik
A	7.5				7.9*	
B	5.7		6.3	5.7	5.8	5.2
B1	4.4		4.8*	4.4	4.5	4.1
B3	1.7			1.7		
B4	1.6			1.7	1.6	
C	2.5			2.1	2.4	
D	1.8				2.1*	
I	15.8	14.9		15.1		
J	7.9					
J1	9.0			8.9		
J2	8.3			8.0		
K	4.5		5.2	4.8	4.4	4.1
K1	4.6		5.2	4.9	4.6	4.2
K2	4.2		4.6	4.5	4.2d	3.8
K3	3.7		4.0*	3.9	3.8d	3.3*
K5	3.6		3.9	3.8	3.7d	3.2*
W	5.9		6.9	5.8	6.1	
X	2.5		2.9	2.5	2.7	
X1			1.5		1.4	
Y			2.5	2.5	2.3	
Z	2.5		2.8	2.7	2.6	

Calymene patustria sp. nov.

	RM Ar6221 Petesvik	RM Ar6222 Petesvik	RM Ar47855 cont. Petesvik	RM Ar27151 cont. Petesvik
B1	7.5*			
J	12.6			
J1	13.5			
K1	6.9			
K2	6.0	5.5		
K3	5.3	4.6		
K5	5.2	4.6		
a				3.1
b				3.5
b1				2.3
b2				2.4
b3				1.4
d				3.8
e				2.6
e1				1.4
g			5.8	
g1			2.6	
h			2.6	
p			0.9	

T. volsoriforma sp. nov.

	GSM Zs63	GSM Zs58	GSM Zs62	GSM Zs65	GSM Z19983	LM 2850 (C)	GSM Z19696
A	13.4*	16.3*			16.1	16.5	
B	9.8*	12.1*		11.3*	12.0	12.8	
B1	7.6	9.2	9.1*	9.3	9.6	10.1	
B2	1.7	2.1		2.0		2.5	
C					7.1	7.1	
C1	8.1	9.9	10.2	10.7*	10.1	11.0	
D	3.6	4.2	3.7		4.1	3.7	
D1	0.6	0.8	0.6		0.8	0.6	
I		37.0d					
J	12.5*	14.0	14.0		13.4		
J1	16.9	19.9	20.0d	20.6	19.7	20.9	
K	8.9	10.7*			11.0	11.0	
K1	8.8	10.7	10.2	11.7	10.5	10.9	
K2	7.1	8.8	8.0	8.8	8.6	9.3	
K3	5.9	6.8	6.5	6.7	7.0	7.1	
K5	5.8	6.7	6.4	6.6	6.6	6.8	
e							6.2
e1							2.7
g		11.2*					
g1		6.3*					
h		4.9*					
p		1.1*					

T. volsoriforma sp. nov.

	GSM Zs61	GSM Zs64
W	20.8d	22.6d
X	6.1	6.6d
X1	3.0	
Y	9.9	
Z	10.4	

<u>T.</u> <u>vulpecula</u> sp. nov.

	DJS/48	DJS/75	DJS/76	DJS/77	DJS/80 (I.)	DJS/79		DJS/78b (C)
A	16.6	15.1	14.6	8.6			a	3.8
B	12.2	10.8	10.4	6.2			b	4.7
B1	9.3	8.3	8.0	4.9			b1	2.9
B2	2.1		1.6	1.2			b2	2.8
C	6.2*						b3	1.4
C1	10.1	9.0	9.0	5.3			d	4.3d
D	4.4	4.3	4.2	2.4			e	3.1
D1	2.2	2.2	2.1	1.2			e1	1.4
I			32.0d	20.4d			e2	0.3
J	14.8	13.3d	14.6d	8.0				
J1	19.8d	18.8d	18.8	11.2d				
K	11.3	9.4	9.8	6.3				
K1	11.0	9.4	9.7	6.0				
K2	8.8	7.7	7.8	5.1				
K3	6.3	5.4	5.7	3.7				
K5	6.0	5.2	5.3	3.5				
W					19.0	21.5		
X					6.2	6.8		
X1					2.9*	3.4		
Y					8.5	9.9		
Y1					1.8*	2.5		
Z					9.2	9.7		

T. nodulosa

	LM 4885	HM A212/1	GSM Zs183	GSM Zs189b	GSM Zs195	RO 1300	DJS/51
A	17.4	16.8	17.2*		17.4		
B	12.5	11.7	12.3*	11.2	12.0		
B1	9.7	8.9	8.6	9.3	8.8		
B2	1.8	1.8	1.8	1.7	2.0		
C		6.4	6.7		6.9		
C1		9.4	9.1	9.7	9.4		
D	4.8	5.1	4.9		5.4		
D1	3.4	3.4	2.8		3.1		
I		32.8					
J	17.3	14.3	15.0	16.0d	15.0		
J1		18.0	21.0d	22.0d	21.5		
K	13.1	10.2	11.5		11.2		
K1	12.3	10.3	10.7	11.0	10.8		
K2	9.7	8.5	9.3	10.0	9.0		
K3	7.1	5.8	6.5	6.7	6.3		
K5	6.7	5.6	6.1	6.4	5.9		
W		23.0				25.7	8.8
X		7.1				7.4	2.7
X1		4.0				3.8	1.5
Y		11.6				10.5	3.6
Y1		2.8				2.3	
Z		13.8				10.6	4.0

<u>T. nodulosa</u> (Shirley, 1933)

	GSM 19642	DJS/49	LM 4902
A		20.1	
B	12.0	14.6	11.8
B1	8.9	11.6	9.0
B2	1.7	2.5	1.8
C		7.0	6.6
C1		11.9	9.4
D		5.5	
D1		4.1	
I	32.3	41.5	
J		17.6	15.1
J1	20.0*	21.8	20.0
K	10.7	13.3	11.7
K1	10.4	12.7	11.2
K2	8.2	10.3	8.8
K3	6.0	7.5	6.1
K5	5.7	7.1	5.6
W	22.1		
X	7.0		
X1	3.4		
Y	10.6		
Y1	2.5		
Z	12.2		

T. nodulosa

	NMW 53.288.G1	DJS/3a	DJS/6a	IM 4877	RO 1302	DJS/47	RM Ar38841
W	34.2						
X	11.1						
X1	5.9						
Y	14.5						
Y1	4.0						
Z	15.2						
a				7.7	6.9	6.0	7.2
b				8.9	7.8	6.5	8.1
b1				5.7	5.3	4.3	5.5
b2				5.4*	5.1	4.6	5.1
b3				2.5	2.1	1.9	2.3
d				9.8	7.2*	7.2	8.4
e				6.2	5.4	5.0	6.3
e1				2.5	2.5	2.1	2.4
e2				0.7			0.4
g		11.3	10.0				12.7
g1		7.0	4.9				6.5
h		4.7	4.8				4.5
p		1.7					1.8