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SILICIFIED MIDDLE ORDOVICIAN TRILOBITES:

Remopleurididae, Trinucleidae, Raphiophoridae, Endymioniidae

By H. B. Whittington

With 36 Plates

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INTRODUCTION AND ACKNOWLEDGEMENTS

In these pages a further portion of the remarkable silicified material from Virginia is described. Lists give the stratigraphical distribution of all the trilobites from the Middle Ordovician of Virginia so far studied. From these lists support is derived for the correlation and classification of Middle Ordovican rocks recently proposed by G. Arthur Cooper. The species of *Raymondella* and *Salteria* described here are the only ones known other than the type species from Scotland, a striking example of the close similarities between some twelve species in the lower Edinburg formation and species of the same age in northwestern Europe. The rocks in each region also contain species of genera not known in the other.

Of the families here dealt with, this is the best preserved material so far known of both mature and developmental stages of the exoskeleton. The protaspis of a remopleuridid from older rocks had previously been described by Ross. The protaspides of five different species of *Remopleurides* are described here, and show a likeness to each other and to the older one. The species of *Remopleurides* occur through some 500-900 feet of limestone in Virginia, about 75 feet separating the Upper Lincolnshire and earliest lower Edinburg occurrences, and perhaps 350 feet separating the latest lower Edinburg and lower Martinsburg trilobite-bearing layers. A continuous record of an evolving series of forms is thus not available, but rather the collections reveal the appearance of new species at different levels and their disappearance at various times. There are two pairs of distinct but closely similar species, one pair comprising *R. asperulus* and *R. eximius* in the upper Lincolnshire and lower Edinburg, the other including *R. caelatus* and *R. plaesiourus* in the lower Edinburg and lower Martinsburg respectively. The pairs are quite dissimilar, and unlike either of the two additional species in the lower Edinburg. Morphological characters common to *Remopleurides* are differently developed in these and in other species — the great morphological detail revealed by the present material suggests the broad limits to the genus here drawn, but blurs distinctions which I might earlier have made (Whittington, 1950b, p. 542) between groups of species. The species of *Robergia* is like other species in this country and northwestern Europe; a few developmental stages are described. *Robergiella* n. gen. is based on fragmentary material, and displays characters intermediate between *Remopleurides* and *Robergia*.

Meraspid developmental stages of trinucleids have been described by several authors, but the present material includes the protaspis of two genera. The new species of *Tretaspis* is closely related to species of the same age from New York and Quebec, and to a younger species from Norway. The development of a raphiophorid was hitherto unknown. The development of four species, each belonging to a different genus, is here described and in one the series begins with the protaspis. The latter, and early meraspides, are like those of trinucleids, and display alae. A close relationship between these two families is thus suggested.

The history of the discovery of these fossils, and my reasons for being indebted to Dr. G. Arthur Cooper of the U. S. National Museum, have been recounted (Whittington, 1956, p. 160). Material collected and prepared by Dr. and Mrs. William R. Evitt has been used in these studies. I am indebted to Dr. Evitt for allowing me to use prints from his negatives, and to Mrs. Evitt for her painstaking sorting of the finest residues. Dr. Ethel D. Currie, Hunterian Museum, Glasgow, kindly loaned the original material of *Ampyxina aldonensis,* and Dr. G. Arthur Cooper allowed me to study the types of *Ampyxina powelli.* I am grateful also to Mrs. Karl Schuele, and to Mr. Ira B. Laby for preparing the enlargements from my negatives and for aiding in mounting the plates. The expenses of this assistance have been defrayed by a generous grant from the Permanent Science Fund of the American Academy of Arts and Sciences. Text-figure 6 was drawn from my sketches by Mr. F. Y. Cheng, and the remaining figures by Miss Margaret Estey.

TERMINOLOGY

The terminology used here is the same as that employed in previous descriptions (Whittington and Evitt, 1954, pp. 11-14; Whittington, 1956, pp. 160-162; Whittington, 1957, p. 423, fig. 1). Since trilobites are bilaterally symmetrical animals, many features of the exoskeleton are paired. Such paired structures have in most cases been described in the singular. When stating that a certain feature appears at "one-third the length" of a part of an exoskeleton, this distance is measured from the anterior end. *Sagittal* (sag.), *Exsagittal* (exs.), and *Transverse* (tr.) refer respectively to the median line, a line parallel to, but outside of the median, and a direction at right angles to the median.

The abbreviations used in the text are given in parentheses. The use of certain other terms may be explained as follows: —

Trinucleidae and Raphiophoridae

Occiput (Stäuble, 1953, p. 87) is applied to the slightly swollen glabellar ring situated between the occipital furrow and the basal lateral muscle area.

Fringe of trinucleids is described using terms devised for harpids by Whittington (1950a). Whittard (1955, pp. 27-29) has introduced a more precise notation for the pits of the fringe. I have followed him in numbering radial rows of pits "R", starting with R_1 which occurs just to the right of the midline and counting outward in arabic numbers towards the postero-lateral part of the fringe.

Pygidium of both raphiophorids and trinucleids has the pleural regions extending horizontally outward and distally bent sharply down so that a narrow portion forms an almost vertically sloping *border*. At the point of flexure of the pleural regions there may be a narrow sharp ridge, here termed the *rim*. The external margin of the border is characteristically sinuous in outline with a broad *median notch*.

Remopleurididae

Some terms used in describing the cephalon are summarized in Text-figure 1.

Glabella. Used here to include the occipital ring, the area enclosed by the palpebral furrows (here termed the median glabellar area), and the glabellar tongue which lies between the anterior ends of the eye lobes; bounded laterally by the axial furrows and anteriorly by the preglabellar furrow. The narrow strip enclosed between the axial furrow and the anterior branch of the facial suture is referred to as the anterior area of the fixed cheek and that in front of the preglabellar furrow as the preglabellar area. *Palpebral rim* and *palpebral furrow* are used in the sense of Ross (1948, p. 574). The narrow wedge-shaped portion of the fixed cheek lying behind the eye lobe and outside the axial furrow is referred to as the posterior area of the fixed cheek. The narrow raised ridge that runs along the outer margin of the eye lobe, on the free cheek, was termed by Warburg

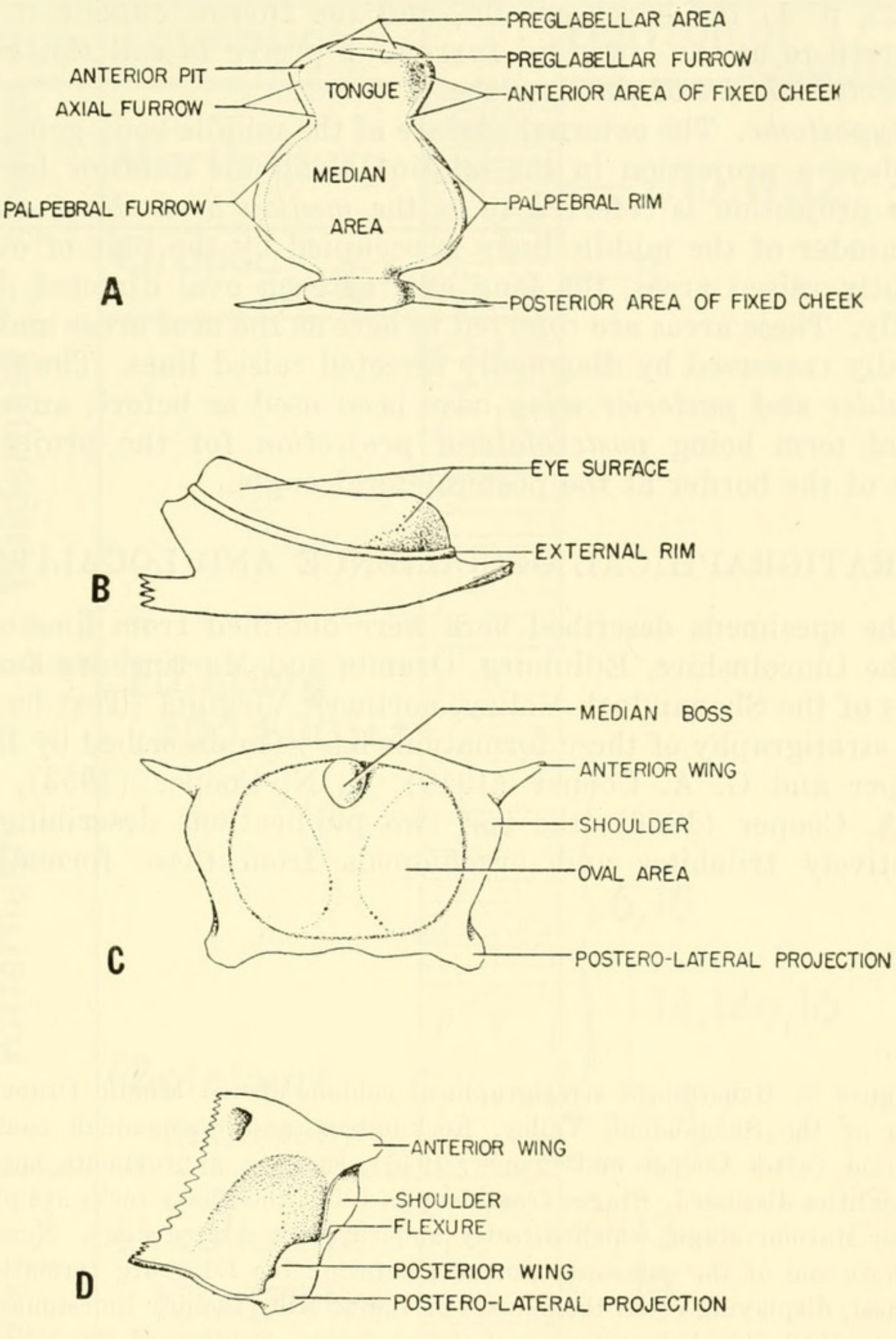


Figure 1. Diagrams illustrating some terms used in describing remopleuridids. A, cranidium (compare Pl. 1, figs. 1, 2). B, lateral view of free cheek (compare Pl. 1, fig. 16). C, exterior view of hypostome (compare Pl. 15, fig. 2). D, oblique interior view of part of hypostome (compare Pl. 15, fig. 3).

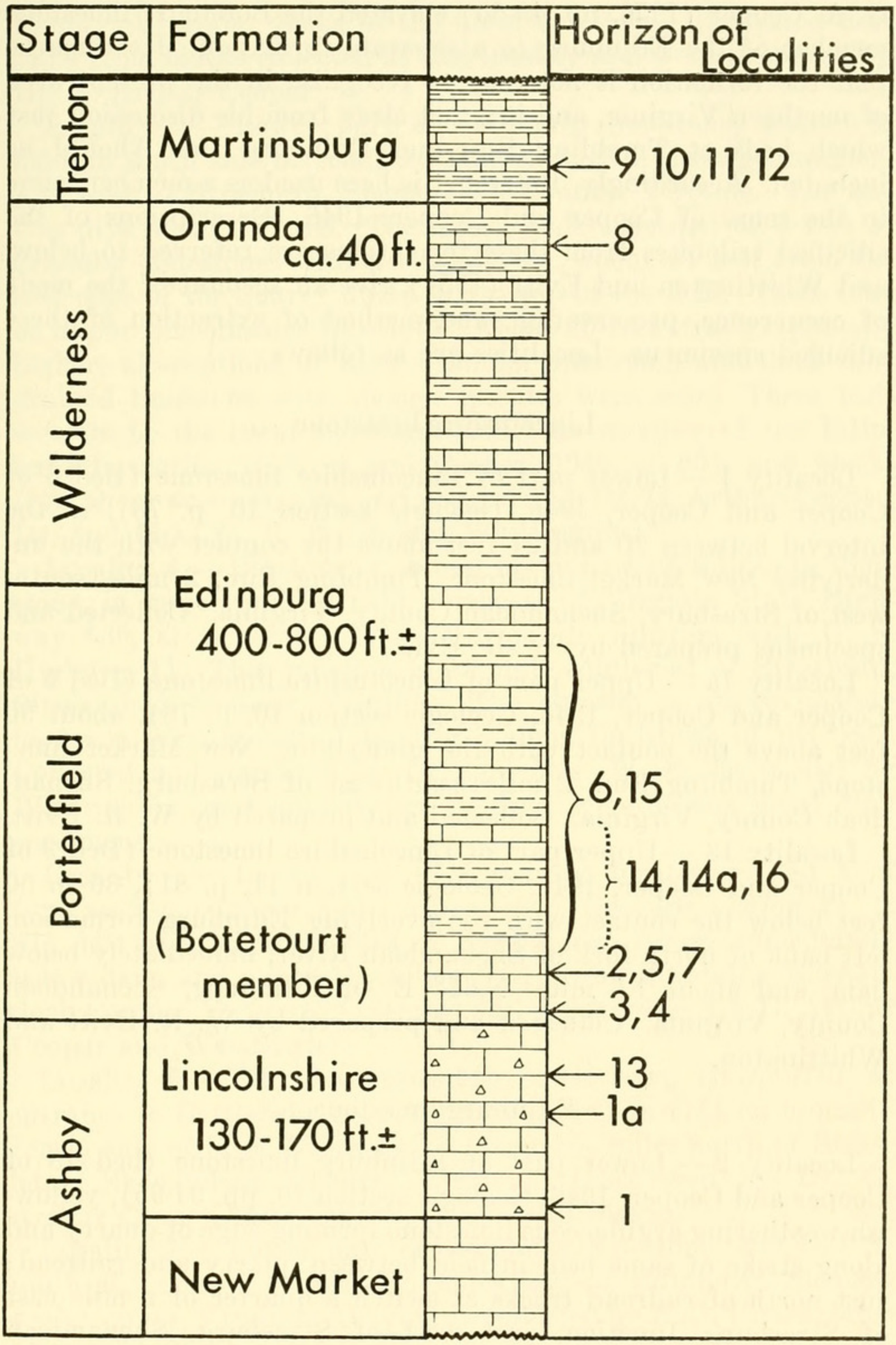
(1925, p. 4) the lower eye lid, and the furrow outside it was referred to as the lower lid furrow. I prefer to call this ridge the *external rim* of the eye lobe.

Hypostome. The external surface of the middle body generally displays a projection in the midline along the anterior border. This projection is referred to as the *median boss.* Most of the remainder of the middle body is occupied by the pair of ovate, slightly raised areas, the long axis of each oval directed diagonally. These areas are referred to here as the *oval areas* and are usually traversed by diagonally directed raised lines. The terms *shoulder* and *posterior wing* have been used as before, an additional term being *posterolateral projection* for the projecting part of the border at the posterolateral angle.

STRATIGRAPHICAL OCCURRENCE AND LOCALITIES

The specimens described here were obtained from limestones of the Lincolnshire, Edinburg, Oranda and Martinsburg formations of the Shenandoah Valley, northern Virginia (Text-fig. 2). The stratigraphy of these formations has been described by B. N. Cooper and G. A. Cooper (1946), B. N. Cooper (1953), and G. A. Cooper (1956), the last two publications describing respectively trilobites and brachiopods from these formations.

Figure 2. Generalized stratigraphical column of the Middle Ordovician rocks of the Shenandoah Valley, Rockingham and Shenandoah counties, Virginia (after Cooper and Cooper, 1946), showing approximate horizons of localities discussed. Stages from Cooper, 1956; the Chazy rocks are placed in the Marmor stage, which directly underlies the Ashby stage. Near the northern end of the outcrop under consideration the Edinburg formation is thinnest, displaying equal thicknesses of Lantz Mills (cobbly limestone) and Liberty Hall (black limestone and shale) facies. Southward the Edinburg thickens and is almost entirely Liberty Hall facies (Cooper and Cooper, 1946, fig. 4).


Stage
Formation
Horizon of Localities
Trenton
Wilderness
Porterfield
Ashby
Martinsburg
Oranda
ca. 40 ft.
Edinburg
400-800 ft.±
(Botetourt
member)
Lincolnshire
130-170 ft.±
New Market
9,10,11,12
8
6,15
14,14a,16
2,5,7
3,4
13
1a
1

G. A. Cooper (1956, pp. 49-50) elevated the Botetourt limestone member of the Edinburg to a separate formation. He remarks that the formation is not easy to recognise in the present area of northern Virginia, and it is not clear from his discussion just which beds at Tumbling Run and Edinburg Dam should be included. Accordingly, Botetourt is here used as a member name in the sense of Cooper and Cooper, 1946. Descriptions of the silicified trilobites from these formations are referred to below, and Whittington and Evitt (1954) give an account of the mode of occurrence, preservation, and method of extraction of these silicified specimens. Localities are as follows:

Lincolnshire limestone

Locality 1 — Lower part of Lincolnshire limestone (Bed 3 of Cooper and Cooper, 1946, Geologic section 10, p. 76), in the interval between 20 and 24 feet above the contact with the underlying New Market limestone, Tumbling Run, 2 miles southwest of Strasburg, Shenandoah County, Virginia. Collected and specimens prepared by W. R. Evitt.

Locality 1a — Upper part of Lincolnshire limestone (Bed 5 of Cooper and Cooper, 1946, Geologic section 10, p. 76), about 90 feet above the contact with the underlying New Market limestone, Tumbling Run, 2 miles southwest of Strasburg, Shenandoah County, Virginia. Collected and prepared by W. R. Evitt.

Locality 13 — Upper part of Lincolnshire limestone (Bed 3 of Cooper and Cooper, 1946, Geologic section 11, p. 81), 30 to 50 feet below the contact with the overlying Edinburg formation, left bank of north fork of Shenandoah River, immediately below dam, and about 1.5 miles N.61° E. of Edinburg, Shenandoah County, Virginia. Collected and prepared by W. R. Evitt and Whittington.

Edinburg limestone

Locality 2 — Lower part of Edinburg limestone (bed 18 of Cooper and Cooper, 1946, Geologic section 19, pp. 94-95), yellowish-weathering argillaceous limestone forming edge of quarry and along strike of same bed, in field between quarry and railroad; just north of railroad tracks at switch a quarter of a mile east of Strasburg Junction, just west of Strasburg, Shenandoah

County, Virginia. Some of the finest specimens illustrated here came from blocks collected at this locality and were prepared by Dr. G. Arthur Cooper

Locality 3 — Lower part of Edinburg limestone, section in field on south side of road, 0.2 mile east of Strasburg Junction, just west of Strasburg, Shenandoah County, Virginia. The section dips about 38° SE. The lowest beds consisted of 6 feet of granular limestones with *Girvanella* sp., about 91 feet from the east edge of the quarry dump at the top of the field. These may be upper Lincolnshire limestone. About 20 feet stratigraphically higher, alternations of dark granular limestone and dark fine-grained limestone with sponge spicules were seen. These beds seem to be the basal Botetourt limestone member of the Edinburg formation (Cooper and Cooper, 1946, p. 80), and blocks from them were collected and prepared by Dr. G. Arthur Cooper, Dr. and Mrs. W. R. Evitt, and Whittington.

Locality 4 — Botetourt member, lower part of Edinburg limestone, in upper part of field northeast of Virginia State Highway 639, at a point 0.25 mile from its junction with U. S. Highway 11. This junction is 0.7 mile southwest of Strasburg, Shenandoah County, Virginia. The outcrop is approximately half a mile southwest of locality 3 along the strike of the beds. Collected and prepared by Dr. and Mrs. W. R. Evitt and by Whittington, and notable for yielding some of the finest tiny specimens.

Locality 5 — Lower part of Edinburg formation, bed 5 of type section (Cooper and Cooper, 1946, Geologic section 11, p. 81), left bank of north fork of Shenandoah River, immediately below dam, and about 1½ miles N.61°E. of Edinburg, Shenandoah County, Virginia. Collected and prepared by Dr. G. Arthur Cooper and Whittington.

Locality 6 — Edinburg limestone, lower part, Hupp Hill, at entrance to Battlefield Crystal Caverns, and in field on opposite (east) side of U. S. Highway 11, about 1½ miles north of Strasburg, Shenandoah County, Virginia. Discovered by Dr. G. Arthur Cooper, later collections by Whittington.

Locality 7 — Lower part of Edinburg limestone, 300 feet ± south 40° east of bridge, 1¼ miles east of Edinburg, Shenandoah County, Virginia. Originally collected by E. O. Ulrich, later (1931) by Charles Butts.

Locality 14 — platy black limestone, Edinburg formation, 500 feet east of Lacey Spring Post Office, Rockingham County, Virginia. Collected and prepared by Dr. G. Arthur Cooper and by Whittington.

Locality 14a — as locality 14, but $3/4$ mi. southwest of Lacey Spring Post Office, in field northwest of road. Collected by C. Butts, prepared by G. Arthur Cooper.

Locality 15 — lower part of Edinburg formation, section in field on south side of road, 0.2 miles east of Strasburg junction, just west of Strasburg, Shenandoah County, Virginia. The beds of locality 3 are about 50 feet thick, and locality 15 is in strata 50 to 180 feet above the top of these. Locality 15 is about the same horizon as locality 6. Collected by W. R. Evitt and Whittington.

Locality 16 — Liberty Hall facies (black limestone) of the Edinburg formation, in field on west side of Virginia secondary highway 617, near house $1/10$ mile north-north-east of junction of Virginia secondary highways 617 and 753, $2\frac{1}{2}$ miles north of Edom and about 8 miles north of Harrisonburg, Rockingham County, Virginia. Collected by G. Arthur Cooper and Whittington.

Oranda formation

Locality 8 — Lower 5 feet of formation, cobbly limestone, in bank and pasture on north side of Virginia secondary highway 777, just west of its junction with Virginia secondary highway 910, and circa 300 yards north of Greenmount church, five miles north of Harrisonburg, Rockingham County, Virginia. Discovered by G. Arthur Cooper, later collections by Cooper and A. R. Loeblich, Jr., W. R. Evitt, and Whittington.

Martinsburg shale

Locality 9 — Road cut, gutter, and loose blocks in pasture on west side of Virginia secondary highway 910, about half a mile north of Greenmount church, five miles north of Harrisonburg, Rockingham County, Virginia. Same as locality 1 of Evitt and Whittington, 1953, p. 55. Collected and prepared by Dr. and Mrs. W. R. Evitt, Dr. G. Arthur Cooper, and Whittington.

Locality 10 — Pasture on north side of Virginia secondary highway 772, about 1 mile east of Greenmount church, five miles north of Harrisonburg, Rockingham County, Virginia. Collected and prepared by Dr. and Mrs. W. R. Evitt.

Locality 11 — Loose blocks in pasture on north side of Virginia secondary highway 616, 1/4 mile east of intersection with Virginia secondary highway 699, and 2½ miles north-northeast of Spring Hill, 7 miles north of Staunton, Augusta County, Virginia. The Oranda formation immediately underlies the lower Martinsburg formation and outcrops a short distance to the west. This is the same locality from which I obtained all the material described by me in 1941. At that time (Whittington, 1941b, p. 492) two localities were given, distant respectively 2½ miles north-northeast, and 3 miles north-northeast, of Spring Hill and Long Glade. Spring Hill is a new name for the settlement formerly called Long Glade, and the confusion probably arose because the blocks of limestone were collected at different times (cf. Evitt, 1953, p. 34). The first blocks were collected by Dr. G. Arthur Cooper, later ones by Cooper and Whittington.

Locality 12 — In field on south side of Virginia secondary highway 753, 1 mile west of intersection with Virginia secondary highway 732, and 3½ miles north-northeast of Spring Hill, Augusta County, Virginia. This locality, visited by Dr. G. Arthur Cooper and Whittington, is one mile northeast of locality 11.

LISTS OF TRILOBITE FAUNAS

These lists have been compiled from previous publications, the present study, and from additional material yet to be described. The abbreviations used after the systematic names refer to citations in the bibliography as follows: W, 41 = Whittington, 1941b; W, 49 = Whittington, 1949; E, 51 = Evitt, 1951; C, 53 = Cooper, 1953; E, 53 = Evitt, 1953; E and W, 53 = Evitt and Whittington, 1953; W and E, 54 = Whittington and Evitt, 1954; W, 56 = Whittington, 1956. These references are in most cases to the original description of species not considered here, but in a few instances are to descriptions of silicified material of previously published species.

Lincolnshire limestone

	Lower	Upper	
Locality	1	1a	13
Dimeropygidae			
Dimeropyge spinifera W and E, 54	x		
Mesotaphraspis inornata W and E, 54	x		
Chomatopyge marginifera W and E, 54	x		
Remopleurididae			
Remopleurides asperulus n. sp.		x	x
Harpidae			
Dolichoharpes reticulata W, 49; E, 51	x		
Cheiruridae			
Heliomeroides teres E, 51	x		
Ceraurinella chondra W and E, 54	x		
Acanthoparypha chiropyga W and E, 54	x		
Holia secristi W and E, 54	x		
Sphaerexochus hapsidotus W and E, 54	x		
Lichidae			
Amphilichas pandus E, 51	x		
Odontopleuridae			
Ceratocephala triacantheis W and E, 54	x		

In addition there are species of proetids, otarionids, asaphids, encrinurids and dalmanitids. The upper Lincolnshire fauna has not been intensively prepared or studied.

Lower Edinburg limestone

Lantz Mills facies, and 20 to 30 feet above base, including Botetourt member at locality 4.

Locality	2	3	4	5	7
Agnostidae					
Trinodus elspethi C, 53	x				x
Dimeropygidae					
Dimeropyge virginiensis W and E, 54	x				x
Mesotaphraspis parva W and E, 54	x	x			
Chomatopyge falcata W and E, 54	x		x		
Proetidae					
"*Proetus*" *strasburgensis* C, 53	x				
Styginidae					
Raymondaspis gregarius (C, 53)	x				

Locality	2	3	4	5	7
Remopleurididae					
Remopleurides caelatus n. sp.	x	x	x		x
Remopleurides caphyroides n. sp.	x	x	x	x	
Remopleurides eximius n. sp.	?	x	x		
Remopleurides simulus n. sp.		x			
Remopleuridid gen. et sp. ind.		x	x		
Harpidae					
Dolichoharpes reticulata W, 49	x	x	x		
Trinucleidae					
Tretaspis sagenosus n. sp.	x	x	x		x
Raphiophoridae					
Ampyx virginiensis	x	x	x	x	
Lonchodomas carinatus	x	x		x	
Ampyxina powelli				x	
Raymondella elegans		x			x
Cheiruridae	x				
Ceraurinella typa W and E, 54	x		x	x	
Acanthoparypha perforata W and E, 54					
Holia cimelia W and E, 54	x	x			
Sphaerexochus pulcher W and E, 54	x				x
Dalmanitidae					
Calliops strasburgensis C, 53	x				
Calliops callirachis C, 53	x				
Odontopleuridae					
Diacanthaspis lepidus W, 56	x	x	x		
Diacanthaspis secretus W, 56	x	x	x		
Diacanthaspis ulrichi W, 56			x		x
Ceratocephala laciniata W and E, 54	x	x	x		
Ceratocephala (Ceratocephalina) tridens W, 56		x	x		
Apianurus barbatus W, 56	x	x	x		
Apianurus glaber W, 56	x	x	x		
Apianurus sp. ind. W, 56	x				
Calipernurus insolitus W, 56	x	x			

In addition there are species of proetids, asaphids, illaenids, other cheirurids, encrinurids, and lichids. Only one small block from locality 5 was prepared.

Lower Edinburg limestone (Liberty Hall facies)

Locality	14	14a	16
Agnostidae			
Trinodus elspethi C, 53			x

	Locality 14	14a	16
Dimeropygidae			
Mesotaphraspis parva W and E, 54			x
Styginidae			
Raymondaspis gregarius (C, 53)			x
Remopleurididae			
Remopleurides caelatus n. sp.			x
Robergia major	x		x
Robergiella sagittalis n. gen., n. sp.	x	x	x
Trinucleidae			
Tretaspis sagenosus n. sp.		x	x
Raphiophoridae			
Ampyx virginiensis			x
Ampyxina powelli	x		
Ampyxina lanceola n. sp.			x
Raymondella elegans			x
Endymioniidae			
Salteria americana	x		
Cheiruridae			
Ceraurinella typa W and E, 54			x
Acanthoparypha perforata W and E, 54			x
Dalmanitidae			
Calliops sp.			x
Odontopleuridae			
Diacanthaspis ulrichi W, 56			x

In addition there are proetids, an asaphid, and an encrinurid. A large number of blocks from locality 14 have been dissolved in acid, but few blocks from 14a.

Lower Edinburg limestone

100-250 feet above base, Lantz Mills facies

	Locality 6	15
Agnostidae		
Trinodus elspethi C, 53	x	
Styginidae		
Raymondaspis gregarius (C, 53)	x	
Remopleurididae		
Remopleurides caelatus n. sp.	x	x
Remopleurides caphyroides n. sp.	x	x
Raphiophoridae		
Ampyx virginiensis	x	
Lonchodomas carinatus	x	

	Locality 6	15
Cheiruridae		
Ceraurinella typa W and E, 54	x	
Acanthoparypha perforata W and E, 54	x	
Dalmanitidae		
Calliops loxorachis C, 53	x	
Odontopleuridae		
Diacanthaspis secretus W, 56	x	
Ceratocephala laciniata W and E, 54	x	
Apianurus barbatus, W, 56	x	

In addition there is a proetid. Little material from locality 15 has been prepared.

Oranda formation, locality 8

Dimeropygidae
Dimeropyge sp.
Otarionidae
Otarion sp.
Trinucleidae
Cryptolithus sp.
Cheiruridae
Ceraurus sp.
Acanthoparypha sp.
Calymenidae
Flexicalymene sp.
Odontopleuridae
Diacanthaspis orandensis W, 56
Diacanthaspis scitulus W, 56
Diacanthaspis aff. *ulrichi* W, 56
Ceratocephala rarispina W, 56
Apianurus barbatus W, 56

In addition were found an asaphid, an illaenid, a dalmanitid, an encrinurid and a lichid.

Lower Martinsburg shale

	Locality 9	10	11	12
Otarionidae				
"*Otarion*" sp. W, 41	x		x	
Asaphidae				
Isotelus sp. W, 41	x		x	x

Locality	9	10	11	12
Remopleurididae				
Remopleurides plaesiourus n. sp.	x	x		x
Trinucleidae				
Cryptolithus tesselatus	x	x	x	x
Cheiruridae				
Ceraurus whittingtoni E, 53	x		x	
Calymenidae				
Flexicalymene senaria W, 41; E and W, 53	x		x	x
Dalmanitidae				
Dalmanitid	x		x	x
Odontopleuridae				
Primaspis ascitus W, 56		x		
Diacanthaspis cooperi W, 56	x	x	x	x

FAUNAL AFFINITIES

Appalachian. The distribution of some of these trilobites in rocks of Middle Ordovician age in the Appalachian Valley between Pennsylvania and Alabama has been discussed by B. N. Cooper (1953). G. A. Cooper (1956) erected five new stages to accommodate the rocks between the Canadian and typical Trenton limestone, and, on the basis of brachiopod studies, gave his reasons for correlations and age assignments of particular formations. He regards the Lincolnshire limestone as younger than the Chazy because it contains only two Chazyan brachiopod genera and five post-Chazyan genera. Of the trilobite genera from the Lincolnshire listed above, *Remopleurides, Sphaerexochus, Amphilichas,* a proetid, sundry asaphids and encrinurids, and the dalmanitid *Calliops* are known in the Chazy. The dimeropygids and such cheirurids as *Ceraurinella, Acanthoparypha* and *Holia* are not known in the Chazyan but range through and above the Lincolnshire, and the Lincolnshire lacks such Chazy forms as *Uromystrum, Vogdesia, Glaphurus, Pliomerops, Heliomera* and other cheirurids. The evidence of the trilobites thus seems to support G. A. Cooper's view that the Lincolnshire limestone is post-Chazyan in age (i.e. Ashby stage, Text-fig. 2) and displays affinities with faunas of the succeeding Porterfield stage.

Many of the Edinburg formation trilobites are like those of the lower Lincolnshire limestone, being different species of the same genera. The Edinburg, Lantz Mills facies, of cobbly, buff-weathering limestone (Cooper and Cooper, 1946, p. 78), has a richer and more varied fauna, however, including *Trinodus, Raymondaspis,* four species of *Remopleurides, Tretaspis,* the raphiophorids and odontopleurids. The typical Liberty Hall facies of black limestone and shale in the lower Edinburg of locality 14 (cf. Cooper and Cooper, 1946, p. 78, fig. 4) has a restricted trilobite fauna unlike that of the Lincolnshire. Locality 16 has an intermediate fauna including typical Liberty Hall elements and many Lantz Mills forms. G. A. Cooper (1956, pp. 43, 50, 61) regards the fauna of the lower Edinburg formation, Botetourt member, as clearly related to that of the Effna formation. The similarity between the trilobites is not great (B. N. Cooper, 1953, Table 1) and the differences may reflect facies differences — the Effna formation is a calcarenite and reef facies, the Botetourt member a dark, granular limestone. The Youngman formation of Vermont is said by G. A. Cooper (1956, p. 32 and Chart 1) to be of the same age as the Botetourt and earliest Edinburg limestone. From the Youngman formation, Kay (1958, p. 83) has recorded *Isotelus* sp., *Illaenus* sp., *Remopleurides* sp., *Lonchodomas* (a species remarkably like that described here), and *Calliops* sp., all typical elements of the lower Edinburg trilobite fauna.

It is G. A. Cooper's belief (1956, pp. 9, 81-82) that the Oranda formation is pre-Sherman Fall (or pre-Shoreham), i.e. latest Wilderness stage and immediately pre-Trenton (Text-fig. 2), and that the brachiopod fauna is similar to that of the lower Edinburg but modified by Trenton elements. The trilobite fauna is of the same type — occurring with the abundant species of Edinburg type are extremely rare examples of typical Sherman Fall genera — *Ceraurus* sp., *Flexicalymene* sp. and *Cryptolithus* sp.. The overlying lower Martinsburg shale, believed by G. A. Cooper (1956, pp. 9, 77, and Chart 1) to be of Shoreham age, yields abundant *Cryptolithus, Ceraurus* and *Flexicalymene,* as well as *Primaspis,* all typical Shoreham genera.

Thus the trilobite faunas of lower Lincolnshire to lower Martinsburg age suggest similar correlations to those advanced by G. A. Cooper on the basis of brachiopods. The Porterfield stage trilobite fauna, however, is not an "exotic fauna that floods into the Appalachians and blots out and absorbs the Lincolnshire fauna" (G. A. Cooper, 1956, p. 8). A large part of it is directly descended from that of the Lincolnshire, but there are some additional new elements. In the Shenandoah valley of Virginia the trilobites hardly suggest the division into Porterfield and Wilderness stages, but this is because silicified trilobites are virtually unknown from the middle and upper Edinburg formation (*Nidulites* and *Camarocladia* zones). Brachiopods are best known from the lower and middle Edinburg formation, and apparently also do not show clearly the Porterfield-Wilderness boundary (cf. G. A. Cooper, 1956, pp. 8-9, 59-60). The change at the end of the Wilderness, into the Trenton, is well marked in the trilobite faunas.

European. The Balclatchie beds of the Girvan district, Scotland, are of about the same age as the lower Edinburg formation (cf. G. A. Cooper, 1956, p. 8), and the Scottish species of *Trinodus, Raymondaspis, Remopleurides, Lonchodomas,* and *Raymondella* are very like those from silicified material in Virginia. Among the trilobites from the Craighead mudstones in the same area in Scotland (Tripp, 1954) are species of *Diacanthaspis, Remopleurides,* and *Calliops* that resemble species from Virginia. The Chasmops series of Norway yields *Raymondaspis, Remopleurides, Ampyx, Lonchodomas,* and *Apianurus* (Størmer, 1940; Skjeseth, 1955, p. 26; Whittington, 1956, pp. 270-271), and the same series in Sweden (Thorslund, 1940) contains *Trinodus, Dimeropyge, Raymondaspis, Remopleurides, Sphaerexochus,* and *Apianurus* (Whittington, 1956, p. 271). From the Kukruse (C_2) stage of Estonia (Öpik, 1937) come *Dimeropyge, Remopleurides,* and *Apianurus* (Whittington, 1956, p. 271). Thus in the Balto-scandian area rocks of a similar age to the Edinburg limestone of Virginia contain a number of species of similar trilobite genera. However, in these European areas there are a number of genera — for example, *Hibbertia, Chasmops, Flexicalymene* — that are either not known in the lower Edinburg of Virginia or appear higher in the succession. Similarly, in Virginia there are species of genera such as *Tretaspis* that appear earlier than in Europe, and other genera that are not yet known from Europe.

SYSTEMATIC DESCRIPTIONS AND DISCUSSIONS

Family REMOPLEURIDIDAE Hawle and Corda, 1847

Subfamily REMOPLEURIDINAE Hawle and Corda, 1847

Genus REMOPLEURIDES Portlock, 1843

Type Species. Remopleurides colbii Portlock, 1843 (for redescription see Whittington 1950b, pp. 540-543, pl. 70, figs. 1, 2, 4, 5).

Diagnosis. Axis of exoskeleton relatively wide. Eye lobe long (exs.), eye surface curved through approximately 180°, anterior part of eye lobe close to, or overhanging, anterolateral cephalic border, posterior part of eye lobe abuts against extremity of occipital ring. Glabella narrow at occipital furrow, in front of this occupying entire area between eye lobes so that palpebral and axial furrows are synonymous, tongue of varying width and length, separated from eye lobe by axial furrow and narrow anterior area of fixed cheek, longitudinal and transverse convexity of glabella variable; three pairs of lateral glabellar furrows visible because exoskeleton is thinner along them, equally spaced from each other and the extremities of the eye lobe, first and second furrows long and gently curved, third furrow short. Shallow anterior pit at anterior extremity of axial furrow. Anterior branches of facial suture curve forward and inward from outer, anterior angle of eye lobe to run along the margin of the cephalon immediately in front of the preglabellar furrow and meet in the midline; posterior branches curve outward and backward, isolating a slim, wedge-shaped posterior area of the fixed cheek that varies in width (tr.). Free cheek subtriangular in outline, posterior margin may run transversely or run outward and forward, a projection adjacent to the posterior branch of the suture defines the outer part of the articulating socket. Position of base of genal spine variable, may be opposite occipital ring or in advance of this position, librigenal spine may be extremely short or long and curved; some species with acute genal angle to free cheek and librigenal spine situated on the lateral border in front of this angle. Hypostome subsquare to transversely subrectangular in outline, convex lateral and posterior borders, anterior and posterior wings present, median boss of variable prominence, oval areas of thinner exoskeleton on middle body; shoulder and posterolateral projection separated by a lateral excavation of variable depth, posterolateral projection may be extended into a blunt spine. Doublure of cephalon broadest anteriorly, crossed by median suture: deep pit in anterolateral portion of doublure, the tip of which reaches the inner surface of the anterior pit.

Thorax (where completely known) of eleven segments, the broad axis tapering back to two-thirds or half its width: large articulating processes and sockets in the axial furrow, pleurae of variable width (tr.), crossed by diagonal pleural furrow: blade-shaped terminal spine of variable length, longer pleurae may be developed on the seventh segment and a median axial spine on the eighth; doublure extends inward to axial furrow. Pygidium of two segments, axis short and rapidly tapering, first axial ring may expand distally and the second axial ring subdivided by a median longitudinal furrow; pleural regions of varying length (sag. and exs.), two pairs of bladelike pleural spines varyingly developed; doublure extends in to tip of axis, median projection from inner edge.

External surface with raised anastomosing lines, may be in a Bertillon pattern on the glabella, elsewhere on the axis running transversely, on the pleural regions running longitudinally or in curves convex forwards: granulation may also be present on the glabella, and rows of tubercles along the posterior edge of the occipital and axial rings. Raised lines, running subparallel to the margins, on the doublure.

Morphology of the holaspid

Morphological features have been summarized in the diagnosis of *Remopleurides*. The developmental series have revealed the limits of the glabella in the holaspis by showing that palpebral furrow and axial furrow, at first separate, become confluent. The three pairs of glabellar furrows are not furrows in the sense of being considerable depressions in the external surface, but are visible because they are lines along which the exoskeleton is thinner (Pl. 5, fig. 2). On the external surface raised lines and granulation are faint or absent along these furrows, and they may be faintly depressed (Pl. 1, fig. 1; Pl. 5, fig. 1; Pl. 8, fig. 5);

on the inner surface they are excavated (Pl. 1, fig. 6; Pl. 12, fig. 14).

Tripp (1954, p. 665) mentioned the presence of a shallow anterior pit in *Remopleurides biaculeatus*, and the presence of a deep pit in the doublure which projected upwards so that the tip rested against the anterior pit. The silicified specimens described here show these features in detail (Pl. 2, figs. 23-25; Pl. 8, figs. 8-10; Pl. 15, figs. 17, 18). Externally the anterior pit is shallow but makes a distinct rounded boss on the inner surface, and there is a depression in this boss. This depression appears to have received the tip of the cone (as seen on the internal surface) extending in from the doublure. The tip of the cone may be rounded and closed (Pl. 8, fig. 9; Pl. 15, fig. 18) or exhibit a minute opening (Pl. 2, fig. 24). The opening may be the result of incomplete preservation or breakage of the thin exoskeleton at the tip. I have observed the pit in the doublure of other species of *Remopleurides* and it is also present in the closely related genus *Hypodicranotus* Whittington, 1952b.

At least the median half of the anterior edge of the hypostome appears to have fitted along a sutural boundary with the inner edge of the doublure of the free cheeks (Pl. 1, figs. 10-12; Pl. 7, figs. 4, 5, 7, 9; Pl. 8, fig. 7). Just inside this edge of the doublure runs a sharp double flexure, strongest near the median suture, dying out a short distance away (Pl. 1, fig. 10; Pl. 2, fig. 23; Pl. 8, fig. 9; Pl. 15, fig. 17; Pl. 17, figs. 3, 10). Distally the edges of hypostome and doublure appear to have separated, that of the former curving above (i.e. dorsally to) the inner edge of the doublure, so that the anterior wing probably projected above and inside this edge. Laterally the inner edge of the doublure of the free cheek is curled over, but this curled portion diminishes and disappears about where the anterior wing lay close to the doublure of the free cheek. There is no wing process, and the anterior wing does not seem to have lain against, or very close to, the anterior boss. The thick, flat edges of the hypostome and doublure of the free cheeks along the hypostomal suture (Pl. 15, figs. 5, 18) do not suggest that movement took place along this suture. Presumably the hypostome was more or less rigidly attached along this suture and held in position by muscles.

If the ventral aspect of the cephalon of the cheirurid *Ceraurus* (Text-fig. 3A; cf. the similar genus *Ceraurinella* in Whittington

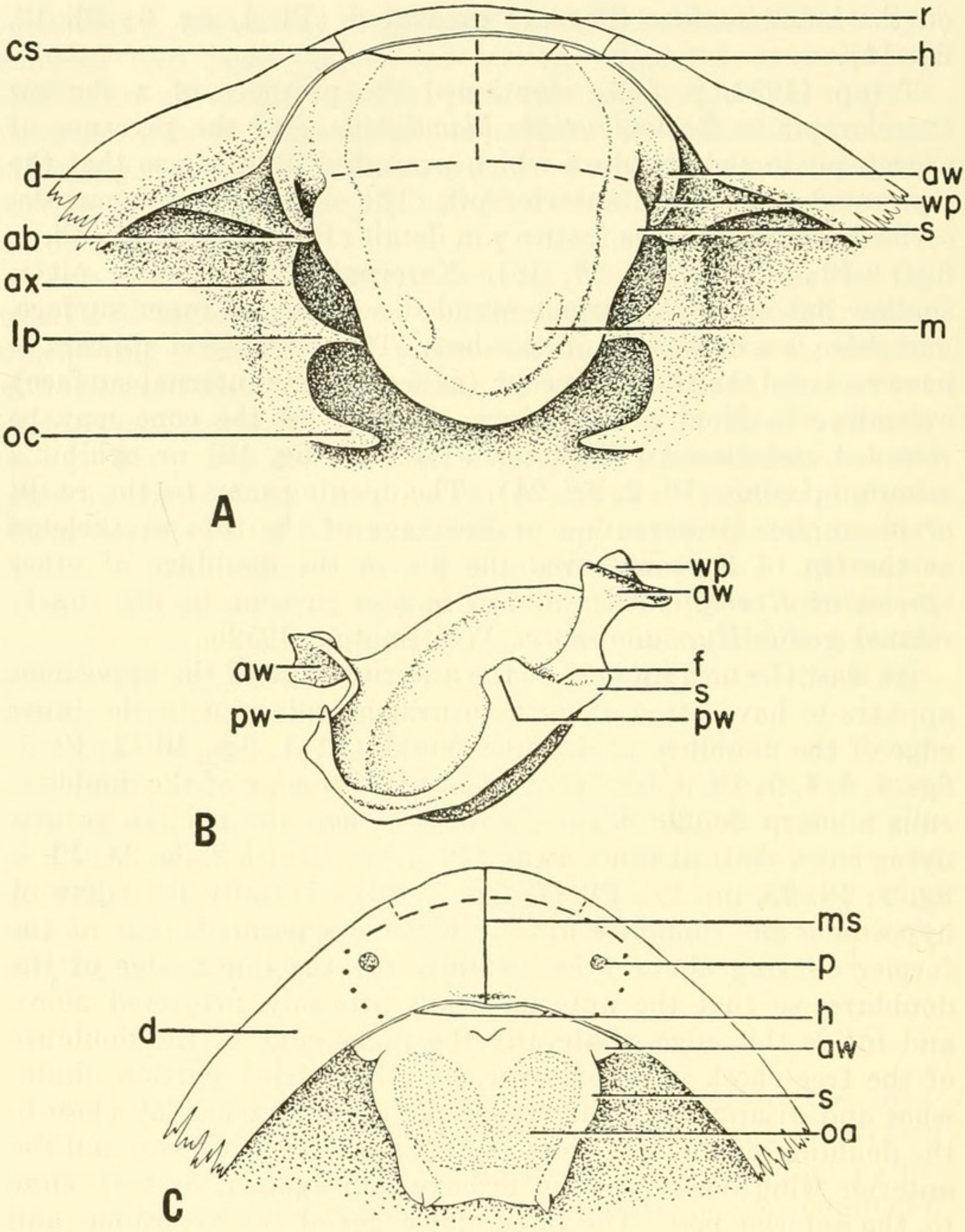


Figure 3. A, ventral view of part of cephalon of *Ceraurus* sp., showing hypostome in position. B, oblique interior view of hypostome of *Ceraurus* sp. C, ventral view of part of cephalon of *Remopleurides caelatus* n.sp., showing hypostome in position. Abbreviations: *ab*, anterior boss; *aw*, anterior wing; *ax*, axial furrow; *cs*, connective suture; *d*, doublure; *f*, flexure crossing doublure; *h*, hypostomal suture; *lp*, ridge formed by first (basal) glabellar furrow; *m*, macula; *ms*, median suture; *oa*, oval area of hypostome; *oc*, appendifer at extremity of occipital furrow; *p*, pit in doublure; *pw*, posterior wing; *r*, rostrum; *s*, shoulder; *wp*, wing process. For explanation of dashed and dotted lines, see text.

and Evitt, 1954, pp. 19-20) is compared with that of *Remopleurides* (Text-fig. 3C) the similarity in structure of the wing process of *Ceraurus* and the pit in the doublure of *Remopleurides* is evident. Both extend dorsally as a cone, the tip lying against the anterior boss. Yet in *Ceraurus* the wing process (Text-fig. 3A, B) is part of the hypostome, while in *Remopleurides* the pit is situated in the cephalic doublure in front of the hypostome. If they are assumed to be homologous structures then the median and hypostomal sutures of *Remopleurides* lie in positions which are shown by dashed lines in *Ceraurus* (Text-fig. 3A). In the drawing of *Remopleurides* (Text-fig. 3C) the position in which the rostral, connective and hypostomal sutures of *Ceraurus* lie is shown likewise by dashed lines, and dots indicate roughly the remainder of the boundary of the part that is included in the hypostome of *Ceraurus*. If one accepts this hypothesis then it follows that:

1) the hypostomal suture in *Remopleurides* and *Ceraurus* is not a homologous but an analogous structure;

2) the portion of the exoskeleton included in the hypostome is not the same in *Remopleurides* as in *Ceraurus*. This may be also true as between *Remopleurides* and other types of trilobites;

3) the anterior wing in *Remopleurides* is not homologous with that of *Ceraurus*;

4) the doublure immediately behind the shoulder in *Ceraurus* is crossed diagonally by a sharp flexure (*f* in Text-fig. 3B), and the inner edge projects as the posterior wing (as in *Ceraurinella*, Whittington and Evitt, 1954, text-fig. 2, pl. 11, fig. 12). The same is true in *Remopleurides* (Pl. 1, figs. 13, 15; Pl. 15, fig. 3; Text-fig. 1d), so that the shoulder and posterior wing appear to be homologous in the two genera;

5) the macula in many trilobites is a relatively small oval area, situated anterior to the inner end of the middle furrow of the middle body, and the exoskeleton over the macula appears to be thinner than surrounding areas and the external surface smooth (Whittington and Evitt, 1954, pp. 16-17). It seems possible that the oval area of the hypostome of *Remopleurides* may be homologous with the macula of other trilobites, for the position is similar and the exoskeleton over the oval area is thinner than adjacent parts. The external surface of the oval area may be traversed by fine, raised lines (Pl. 1, fig. 10; Pl. 4, figs. 3, 4)

or may appear smooth (Pl. 7, fig. 5; Pl. 15, fig. 2; Pl. 17, fig. 18). If it is homologous with the macula of other trilobites then it is exceptionally large in *Remopleurides* (compare illustrations in Lindström, 1901 and Whittington and Evitt, 1954).

6) It has been argued (Whittington and Evitt, 1954, p. 20) that in trilobites the antennule was attached to the anterior boss and curved downwards and forwards beside the hypostome, passing through the lateral notch. This may have been the case in *Remopleurides*, but if so the antennule was directed at first backward, and then curved downward, outward and presumably forward, passing between the shoulder and anterior wing.

In posterior view the hypostome shows the doublure projecting upward, with a small lateral notch beside a larger, deeper, median scallop, and the doublure at this scallop is not upwardly directed but curled over so that the inner edge is directed forward (Pl. 1, figs. 14, 15; Pl. 4, fig. 30; Pl. 15, fig. 5; Pl. 17, figs. 21-23). This median scallop is suggestive of the position of the mouth.

A median axial spine is present on what is most probably the eighth thoracic segment of all the species described here, and is characteristic of other species. In *Remopleurides eximius* and *R. asperulus* the pleurae of the seventh thoracic segment are longer than those of the other pleurae. A specimen from Eire referred to *R. colbii* (Whittington, 1950b, pl. 69, figs. 5, 6) also has the thoracic pleurae of the eighth segment elongated. It may be that this character is a manifestation of sexual dimorphism, and not a specific character, but specimens without such spines do not occur at localities 1a and 13 with *R. asperulus*. The possibility that the specimens here called *R. simulus* are sexual dimorphs of *R. eximius* is discussed under the heading *R. simulus*. Compared to trilobites belonging to other families in the silicified material from Virginia, there are a remarkable number of specimens of *Remopleurides* in which up to as many as nine thoracic segments are linked together with the pygidium (Pl. 12, figs. 15-18; Pl. 14; Pl. 15, figs. 6-8, 11, 12). Perhaps the long articulating half rings and the prominent axial articulating bosses and sockets hold the segments of the (cast?) exoskeleton together more firmly than is the case in many other trilobites. The photographs of such specimens and of single segments (Pl. 2, fig. 5; Pl. 12, fig. 16; Pl. 17, fig. 16) show the facet — the smooth anterior and anterolateral part of the pleura that fits during enrollment beneath the preceding segment. A similar facet is present on the pleural regions of the pygidium (Pl. 15, fig. 14). There is in the doublure of each pleura a depression along the posterior margin, bounded by a sharp change in slope (Pl. 2, fig. 8; Pl. 9, figs. 4, 8; Pl. 12, fig. 17). This depression receives the facetted portion of the following pleura during enrollment. In species such as *R. eximius* and *R. simulus,* in which the genal angle is about opposite the occipital ring, a similar depression is present in the doublure of the free cheek (Pl. 17, fig. 10). During enrollment the facet can move beneath the preceding segment as far as the sharp flexure that limits the depression; that is, the sharp flexure that forms the anterior edge of the depression in the doublure acts as a limit to the possible amount of enrollment. This is well illustrated by the nine segments and pygidium of *R. simulus* (Pl. 17, figs. 12-14). It would appear probable from an examination of this specimen in ventral aspect that the limit of enrollment had been reached for this portion of the thorax. If this is so, even allowing for a further two segments in the thorax, it seems that *R. simulus* could not have enrolled so that the pygidium was closely pressed beneath the cephalon — as is the case in a great many trilobites. An approximately similar amount of enrollment, that is, the thorax curved through about 180°, is shown by the type specimen of *R. rugicostatus* Raymond, 1925 (Pl. 18, figs. 26, 27). In *Hypodicranotus* (Whittington, 1952b), a genus closely related to *Remopleurides,* far less enrollment was possible because of the exceptional size of the hypostome.

Discussion of Development

Protaspis. The spherical form, convexity and definition of axis, lateral cranidial outline, and three pairs of prominent spines of the protaspides attributed to four species described herein (Pl. 3, figs. 1-5; Pl. 5, figs. 18-20; Pl. 10, figs. 15, 18-20; Pl. 11, figs. 1-4; Pl. 13, figs. 1-4, 10) recall at once the protaspis of *Menoparia* (Ross, 1951, pp. 579-583, pl. 81, figs. 1-9; 1953, pp. 634-635). It is because of this resemblance, and their likeness to larger members of the developmental series, that they are placed in *Remopleurides.* In the case of *R. asperulus* and *R.*

plaesiourus no other species of *Remopleurides* occurs at the same horizon, and there can be little doubt regarding the identification. *Menoparia* is from rocks of lower Ordovician age and I consider (Whittington 1959, p. O329) that it belongs to a separate subfamily of remopleuridids from that which includes *Remopleurides*. This type of protaspis may well be common to the family. It has been demonstrated that in the species here described the median pair of spines are fixigenal, lying immediately in front of the faint furrow that divides the cephalic from the protopygidial portion (Text-fig. 4). It may be that the corresponding spines in the protaspis of *Menoparia* also are fixigenal, and do not belong to the protopygidium, as Ross thought. In the protopygidium of the protaspis of *Menoparia*, Ross described the axis as possessing two segments. In the protopygidium of *R. caphyroides* more divisions can be seen clearly, five axial rings and a terminal portion. The pleural regions of the protopygidium of *R. eximius ?* (Pl. 16, figs. 3, 7, 9) are subdivided faintly by bands of granules. Along the posterior margin of the protopygidium in all species a row of five pairs of tiny spines is characteristic, and in *R. caelatus, R. plaesiourus* and *R. caphyroides* the outer pair is larger and in advance of the others. In *Menoparia* and *Remopleurides* (Text-fig. 4) the cephalic sutures follow a scalloped course, outlining the palpebral lobe and the position of the two branches of the suture. In the protaspides of neither genus are the free cheeks and hypostome known.

Degree 0. Meraspides of this degree (Pl. 3, figs. 7-15; Pl. 5, figs. 16, 17, 21-23; Pl. 10, figs. 8-14, 16, 17; Pl. 13, figs. 5-7, 11-15; Pl. 16, figs. 8, 10-17; Text-figs. 5, 6) retain the long anterior cephalic spines (with the possible exception of *R. asperulus*) and a tiny remnant of the fixigenal spine in *R. caelatus, R. plaesiourus* and *R. caphyroides*. The transitory pygidium of the latter three species retains only four pairs of marginal spines, but there are five pairs in *R. asperulus* and *R. eximius?*. The axis displays five axial rings (six in *R. asperulus* and *R. eximius?*) and a strongly convex terminal portion. These specimens are remarkably like the corresponding developmental stages of *Menoparia* described by Ross (1953, pp. 634-635, pl. 62, figs. 6, 7, 9-11, 13, and 16) and I think there is little doubt but that the originals of Ross' figures 7, 9, 10, 11, 13, and 16 are the smallest transitory pygidia of *M. genalunata*. They are extremely similar in form to those of *Remopleurides caelatus*, *R. plaesiourus*, and *R. caphyroides*, displaying five axial rings and a strongly convex terminal portion of the axis. The posterior margin bears five pairs of tiny spines rather than four. Ross does not mention the presence of the pair of tiny tubercles near the anterior margin of the glabella in either the protaspis or the smallest cranidia. However, a pair of such tubercles appears to be present at the anterior end of the meraspid glabella in the original of Ross' (1953) plate 62, figure 6. The presence of these tubercles is another striking similarity to *Remopleurides*.

Larger cranidia. Specimens in this size series cannot be assigned to particular degrees. The smallest are little larger than those of degree 0, and lack the anterior cephalic spine (compare Pl. 3, fig. 9 with Pl. 3, fig. 16; Pl. 5, fig. 16 with Pl. 6, figs. 1-4; Pl. 10, figs. 8, 9, 11 with Pl. 10, figs. 5-7; Pl. 13, fig. 5 with Pl. 13, fig. 17). This spine is reduced as abruptly as between the corresponding stages in *Menoparia* (Ross, 1951, pl. 81, figs. 12, 14). The reduction of fixigenal and protopygidial spines between the protaspis and Degree 0 of *Remopleurides caelatus*, *R. plaesiourus*, and *R. caphyroides* is equally as abrupt. Odontopleurids also show loss of spines between developmental stages, in this case the loss of the fixigenal spine between degree 0 and immediately succeeding degrees (Whittington, 1956, text-figs. 11, 22).

In the smallest post-degree 0 cranidia of *Remopleurides* the palpebral rim is well defined and there is a crescentic portion of the fixed cheek enclosed between the axial furrow and the palpebral furrow (e.g. Pl. 3, fig. 16; Pl. 6, figs. 2, 3; Pl. 13, fig. 17). Such an area is present at a similar developmental stage of *Menoparia* (Ross, 1951, pl. 81, fig. 14), and is reduced in large cranidia by expansion of the glabella (Ross, 1953, pl. 62, fig. 4), but never disappears. In *Remopleurides*, on the other hand, the glabella rapidly expands between the eye lobes and the crescentic area narrows and then disappears, so that the axial and palpebral furrows approach and merge into a single furrow (Pl. 4, figs. 1, 7, 9, 14; Pl. 6, figs. 2, 3, 5, 8, 11, 12; Pl. 13, figs. 17, 20, 24, 28). Other changes that take place in this size series are the general increase in convexity of glabella, both longitudinally and transversely, and the reduction in width (tr.) of the anterior area of the fixed cheek.

Transitory pygidia. In *Remopleurides caelatus* the next transitory pygidia known after those of degree 0 are believed to belong to degrees 5, 6, and 7, and have a long median axial spine (Pl. 4, figs. 5, 6, 13, 16-18, 22). In the development of *Menoparia*, Ross (1953, pl. 62, fig. 20) found a similar type of pygidium to be next in the series. In *R. caelatus* no intermediates are known between the degree 0 and degree 5 transitory pygidia. It is possible that the absence of such specimens implies that they may not have existed; that is, that there was a simultaneous release of four segments into the thorax so that the degree 0 transitory pygidium was succeeded by that of degree 5. In the material at hand the median axial spine appears suddenly and is of extraordinary length. It must develop, perhaps abruptly between moults, from the region represented by the strongly convex terminal axial portion of the degree 0 transitory pygidium (Pl. 3, figs. 10-13, 15). Transitory pygidia of degrees 8 to 10 (Pl. 4, figs. 23-25, belonging to the developmental stages after the release of the segment bearing the median axial spine into the thorax), progressively approach the appearance of the true pygidium and do not have the strongly convex terminal axial portion of the degree 0 transitory pygidium.

Discussion. The development of *Remopleurides* is best known from *R. caelatus*, the less complete developmental series of other species showing, however, that they are similar. The remarkable parallels that have been drawn between the development of the Lower Ordovician species of *Menoparia* and Middle Ordovician species of *Remopleurides*, serve to illustrate the principle that related animals display similar early developmental stages. A comparison between the illustrations given here, and those of Ross, shows that the protaspides and to a lesser extent meraspid degree 0 have a family resemblance to each other. Subfamily and generic characters are visible at immediately succeeding degrees — for example, the shape of the glabella, width (tr.) of the anterior area of the fixed cheek, length (sag. and exs.) of the preglabellar area, form of the pleural regions in *Menoparia*. When comparison is made between the developmental series of the new species of *Remopleurides,* it is evident that specific characters can be picked out even in the protaspis. The developmental series of *R. caelatus* and *R. plaesiourus*, and of *R. asperulus* and *R. eximius* are similar to each other, as are the holaspides. Both developmental series and holaspis of *R. caphyroides* are distinctly different.

Remopleurides caelatus n.sp.

Plates 1-3; Plate 4, figures 1-25; Text-figures 4, 5

Holotype. USNM 137675 (Pl. 1, figs. 1, 2), locality 2.

Other Material. Paratypes USNM 137676a-e; all figured specimens in U. S. National Museum.

Geological Horizon and Localities. Edinburg formation, localities 2-4, 6, 7, 15, 16.

Description. Cephalon of outline, excluding librigenal spines, sub-oval, maximum width greater than length (sag.). Glabella of length slightly greater than maximum width, which is across a point about three-fifths the length. Occipital ring widest (sag.) at mid-line, decreasing progressively in width outward, small median tubercle adjacent to occipital furrow. Latter deep medially, rising vertically on anterior side to median glabellar area; distally where it runs along margin of palpebral rim, the occipital furrow is shallow. Median glabellar area gently convex, descending abruptly (especially postero-laterally) to palpebral furrow. Three pairs of lateral glabellar furrows are visible because the exoskeleton is thinner, being excavated on the inner side (Pl. 1, figs. 5, 6). First and second furrows similar in length, curvature of first stronger, directed inward and backward; distal part of first furrow situated in line with maximum width of median glabellar area, furrow becomes wider inward; second furrow distally of similar width to first, but tapering inward; third furrow short, sub-oval in outline, situated in line (exs.) with inner part of first furrow, the three furrows spaced about equidistantly. Glabellar tongue of same width at base as base of median glabellar area, gently convex, widening forward to anterior extremity, across which it is moderately convex; bounded laterally by axial furrow, which is continuous with preglabellar furrow. Latter furrow becomes progressively shallower and closer to anterior margin of tongue as it runs inward, and dies out before reaching mid-line (Pl. 1, fig. 2). In anterior view outline made by anterior margin of preglabellar area is obtusely angulate (Pl. 1, fig. 2).

Eye surface gently convex transversely, moderately convex longitudinally, more strongly curved in posterior than anterior half; external surface with many tiny, low facets arranged in diagonal lines (Pl. 2, fig. 22). Palpebral rim (Pl. 1, figs. 1, 2) widest adjacent to posterolateral part of median glabellar area, narrowing progressively forward to a minimum width where it joins anterior area of free check, latter merges with preglabellar area; palpebral rim narrows abruptly as it descends to occipital furrow. Anterior branch of suture runs inward in a curve to mid-line; posterior branch runs beside antero-lateral extremity of occipital ring, then out across cheek just inside posterior margin for a short distance before turning to cut the margin immediately outside the fulcral articulating socket (Pl. 1, fig. 5). Cheek outside eye lobe narrow, outward-sloping, separated from eye surface by convex external rim of eye lobe; broad base of librigenal spine in line (tr.) with posterior part of median glabellar area, spine tapers back to sharp point. Inside base of librigenal spine cheek depressed beside external rim of eye lobe, but outer part convex and extended posteriorly in a rounded projection which lies immediately outside the articulating socket (Pl. 1, fig. 4).

Doublure of cephalon includes that beneath occipital ring and that which extends around free cheek, which is narrow postero-laterally, but widens progressively to the mid-line, where it is crossed by the median suture. At the inner edge, for a short distance on each side of the median suture, there is an upward angulation in the doublure (Pl. 1, fig. 10; Pl. 2, fig. 23). Beneath the eye lobe the innermost part of the doublure is thinner and is curled over, the curled portion being widest anteriorly. The edge of the doublure proximal to the curled part is thick and broad (Pl. 2, fig. 23), this edge being that along which the hypostomal suture runs. In the external surface of the doublure, and lying in the same line (exs.) as the outer end of the hypostomal suture, is a pit (Pl. 1, figs. 10, 11). On the inner surface of the doublure this pit appears as a cone, inclined so that the apex lies close to the angulation in the beginning part of the anterior sutural branch. The apex of the cone is broken in many specimens but appears to have a minute opening at the tip when undamaged (Pl. 2, figs. 23, 24). It seems that the tip rested in a pit in the inner surface of the cranidium, at the junction of the axial and preglabellar furrows, which appear as low ridges on the inner surface (Pl. 2, fig. 25).

Hypostome gently convex, maximum width, across anterior wings, greater than length. Middle body not separated from anterior border by border furrow, but laterally outlined by narrow furrow and posteriorly by broader, shallower furrow. Most of middle body occupied by oval areas, most convex posteriorly, and oriented with long axis diagonal; the exoskeleton over these areas is thinner, so that they are more clearly outlined on the inner surface. The subtriangular strip separating the oval areas is not convex. Median boss short, blunt, backwardly directed. Anterior wing a short, rounded projection of noticeably thinner exoskeleton, lacking a wing process. Inner edge of lateral border a sharp ridge, this ridge continued across postero-lateral border and into base of short, blunt spine; posterior border wider than lateral. Exoskeleton at inturned, upwardly-directed edge of lateral and posterior borders thin, the edges scalloped (Pl. 1, figs. 12-15); in front of the posterolateral projection this exoskeleton crossed by a flexure and part of the inner edge is twisted and projects to form the posterior wing; the edge of the portion along the posterior border displays a broad, deep median notch, outside the edge of which is a small, semicircular notch. The broad, flat anterior edge of the hypostome at the suture is inclined forward medially, twisting to incline back laterally, and thus fits close against the correspondingly inclined surface of the suture on the free cheek (Pl. 1, figs. 11, 12).

Dorsal external surface of exoskeleton, except in furrows, bearing fine raised lines in Bertillon pattern which varies little between individuals. Minute tubercles are also scattered over the surface, and become coarse and readily visible on the glabella adjacent to the palpebral and occipital furrows, and along the posterior edge of the occipital ring. On the doublure and genal spine (upper and lower surfaces) the Bertillon lines run parallel to the margins and heavier terrace lines occur with them. External surface of hypostome bearing lines that run sub-parallel to the margin on the borders, but run longitudinally on the middle body. These lines are stronger than the Bertillon lines of the glabella, and on the borders especially are of equal strength to the terrace lines. Because of the thinness of the exoskeleton over the oval areas the lines are prominent over these areas and help to outline them.

Number of thoracic segments unknown, but eleven is typical for the genus. Axis moderately convex, tapering back, width more than half, and posteriorly three-quarters, of that of thorax. Axial ring sloping forward medially, gently inflated distally, lateral margin semicircular in outline and descending vertically to axial furrow. Narrow articulating furrow and long (sag.) articulating half-ring. Median axial spine (Pl. 2, figs. 11, 12, 18) on fourth segment in front of pygidium (? eighth in thorax) directed backward just above thorax, sharp point extending to, or beyond, tip of pygidium, ventral side flattened, dorsal convex. Inner part of pleura narrow (tr.) in anterior segment, diminishing progressively in width posteriorly. Outer part of pleura gently sloping in anterior segments, slope increasing posteriorly; outline subrectangular in anterior segments, with rounded antero-lateral corner and small point on postero-lateral corner; outline changes progressively posteriorly as outer part of pleura is more backwardly curved and drawn out into a longer point. Fulcral articulating socket and process, and adjacent edges of inner part of pleura, strongly raised; apex of triangular flattened areas of inner part of pleura between them leads into a deep depression immediately in front of, and extending outside of, fulcral socket: this depression appears to constitute the pleural furrow, which dies out rapidly distally. Axial socket and process small. Doublure extends inward to fulcrum, except along posterior edge where a narrow tongue continues inward along outer edge of fulcral articulating socket; doublure is bent upward at inner edge, and inner posterior portion is crossed transversely by a sharp flexure, the vertical portion of the flexure facing posteriorly. Because of this flexure an inner, posterior part of the doublure forms a depression which accommodates the antero-lateral part of the succeeding segment during enrollment. The amount of angular movement possible between the segments is thus limited, and in those following the axial spine it is slight.

Pygidium subrectangular in outline, length greater than width. Convex axis semicircular in outline, width three-quarters that of pygidium at anterior margin, but extending little more than one-quarter of length, divided into two rings. First ring shortest and slightly depressed (sag.) in mid-line, articulating furrow running in curve concave forward; first ring furrow more strongly curved and outline concave posteriorly except distally, where it runs transversely; lobate outer portion descends vertically to axial furrow. Second ring bilobate, with a broad, deep median depression. Articulating furrow deepest distally, articulating half-ring long (sag.). Pleural regions gently convex medially, descending vertically to lateral margins, prominent articulating boss at antero-lateral corner, outside and below which is facet; pleural and interpleural furrows absent, posterior margin drawn out into two pairs of pleural spines, the inner pair the larger. Broad doublure, inner part of which is curved dorsally, so that margin lies immediately ventral to sharp flexure at margin of axis. There is some individual variation displayed by the pygidium — in the degree of inflation of the axis, and particularly in the outline, degree of inflation, and relative length of the inner pair of pleural spines. In the original of Plate 2, figure 14, the inner pleural spines are inflated, separated at the base by a deep cleft, and much longer than the outer pair; in the original of Plate 2, figure 20, the inner spines are relatively shorter and not inflated; in the original of Plate 2, figure 15, though inflated, the inner spines are relatively short and blunt.

External surface of posterior margin and inflated distal part of axial rings of thorax and pygidium tuberculate, less conspicuous tubercles may be scattered over pleural regions. Except in furrows and on articulating half ring Bertillon lines run transversely on axial rings and diagonally on pleurae of thorax, subparallel to margin on pleural region. On median axial spine terrace lines run longitudinally, and stronger ones occur at intervals. Similarly, strong terrace lines run longitudinally on thoracic doublure and subparallel to margins of pygidial doublure.

Development

Protaspis. Two complete and 15 broken specimens of a protaspis from locality 6, and 1 and 6 broken specimens from localities 3 and 4 respectively, have been obtained. This protaspis is exceedingly like that of the closely related younger species *R. plaesiourus*.

Protaspis (Pl. 3, figs. 1-5; Text-fig. 4) subspherical in shape, excluding spines maximum length 0.62 mm., maximum width 0.81 mm., maximum height 0.85 mm. Cephalon and protopygidium subequal in size. Occipital ring of width (tr.) about one-third total width, defined posteriorly by shallow ring furrow, anteriorly by extremely faint occipital furrow, and set off from pleural region by its convexity. Axial furrow in front of occipital ring is indicated by change in slope between gently convex glabella and cheek; axial furrows diverge slightly forwards and run in a straight course to margin. Glabella extends to anterior

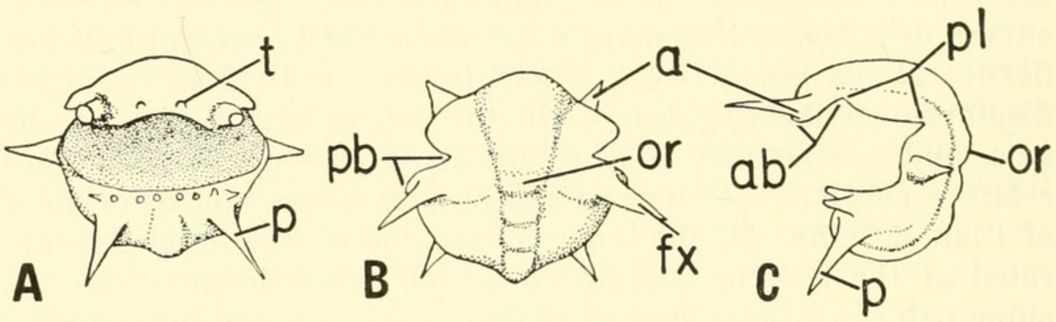


Figure 4. *Remopleurides caelatus* n.sp. A, B, C, protaspis, lacking free cheeks and hypostome, anterior, posterior, and left lateral views, X 26 (compare Pl. 2, figs. 2, 4). Abbreviations: *a*, anterior cephalic spine; *ab*, anterior branch of suture; *fx*, fixigenal spine; *or*, occipital ring; *p*, postero-lateral spine on protopygidium; *pb*, posterior branch of suture; *pl*, palpebral lobe; *t*, tubercle.

edge of shield, which is bent down. Pair of tiny tubercles on anterior slope. Fixed cheek gently convex and outward-sloping, palpebral lobe not raised or defined other than by long, curved sutural margin; anterior branch of suture runs from palpebral lobe forward and outward, then curves inward to margin; posterior branch runs in "S" curve and is directed more strongly outward. At anterolateral corner of fixed cheek there is a thick spine directed forward and slightly outward; at posterolateral corner there is a spine of similar size, the fixigenal, directed backward and more strongly outward. There is only the faintest trace of a transverse furrow, directed outward and slightly back, separating fixed cheek from pleural region of protopygidium, and running out immediately behind the fixigenal spine to reach the margin where it is cut by the extremity of the posterior sutural branch. Free cheek, cephalic doublure, and hypostome unknown. Protopygidium subrhomboidal in outline, well-defined, gently convex axis less than one-third total width, tapering only at blunt tip at posterior margin. In the complete protaspis three axial rings of about equal length (sag.) to the occipital, and a longer tip, may be distinguished. In some broken specimens (Pl. 3, fig. 6) there are five axial rings in front of the tip. Pleural region slopes gently to lateral margin, but posterolaterally and beside tip of axis is bent down vertically, prominent spine at posterolateral corner is situated at upper edge of this flexure. Doublure narrow and curled under, tiny median notch, greatest width posterolaterally, diminishing in width anteriorly to disappear at anterolateral corner. Along posterior margin of pygidium, behind main pleural spines, are 4 pairs of tiny spines, the middle pair close together at base of notch in doublure, the outer pair largest, and directly behind main spines.

Degree 0. Reconstructed (Text-fig. 5) from the smallest cranidia, free cheeks and transitory pygidia (Pl. 3, figs. 7-15, 17, 18), all of which are like those of the younger species *R. plaesiourus*. Cranidia are known from localities 3, 4, and 6, free cheeks from 3 and 4, transitory pygidia from 2-4, 6, 7, 15, and 16.

Differs from protaspis most obviously in better definition and subdivision of axial region, in reduction of fixigenal spine to a small nub, and absence of main posterolateral spines on transitory pygidium. The longitudinal convexity of the cephalon is such that, if the posterior margin of the occipital ring is oriented in the vertical plane, then the anterior slope of the glabella is vertical. The longitudinal convexity of the transitory pygidium and inclination of the articulating half ring is such that the position relative to the cephalon gives a subspherical shape to the exoskeleton. In several specimens a pair of small tubercles may be seen on the glabella, situated in line with the bases of the anterior cranidial spines and near the ill-defined glabellar margin. Palpebral lobe slightly raised above adjacent part of fixed cheek, notably posteriorly, where the angle the margin makes with the posterior sutural branch is more acute and more deeply indented than in the protaspis. Some specimens suggest the presence of a faint, narrow palpebral rim. Free cheeks of smallest size (Pl. 3, figs. 17, 18) fit approximately, and are separated by median suture. The anterior branch of the suture has the characteristic curve so that the dorsal surface of free cheek narrows and disappears at mid-line. Outside eye lobe free cheek of uniform width and lateral outline consequently a convex curve; librigenal spine arises from border at a point opposite two-thirds the length (exs.) of the eye lobe, is broad at the base

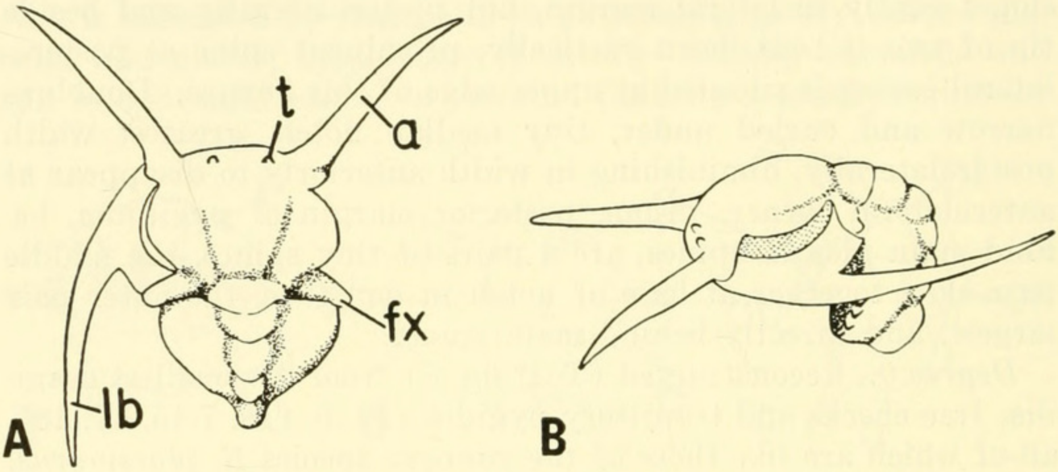


Figure 5. *Remopleurides caelatus* n.sp. Outline reconstruction of degree 0 individual, right free cheek omitted. A, exterior, B, oblique exterior view, X 26. Abbreviations: *a*, anterior cephalic spine; *fx*, greatly reduced fixigenal spine; *lb*, librigenal spine; *t*, tubercle. Based on originals of Plate 3, figures 9, 12.

and tapering. Projection from inner part of posterior border of free cheek not developed. Eye surface narrow (tr.), facets relatively large, about 8 in a diagonal row. Doublure relatively broad in front of librigenal spine, narrow behind, inner margin excavated in broad curve along hypostomal suture, pit in doublure adjacent to extremity of this suture, pit appearing on inner surface as low, blunt cone.

Hypostome unknown.

Transitory pygidium subcircular in outline, strongly convex (sag. and tr.), most strongly so posteriorly. Width of axis about one-quarter maximum width of transitory pygidium, gently convex in anterior part, which is divided by furrows into a prominent articulating half-ring and five axial rings. Rings decrease in length and width posteriorly, the fifth markedly shorter than those in front of it; posterior part of axis strongly convex, undivided, tip steeply sloping. Four pairs of short spines along postero-lateral margin of pleural regions, doublure narrow, curled.

Comparison of this transitory pygidium with the protopygidium of the protaspis shows the strong resemblance in outline and form between the two. Chief changes are the more convex axis, better definition of rings, and lack of main pleural spines in degree 0.

Further development of cephalon. Cranidia of length (sag.) 0.85 (Pl. 4, figs. 1, 2) to 0.97 mm. (Pl. 3, fig. 16) from localities 2, 6, 15 seem to represent the next stage of growth. Occipital ring is wider (tr.) than the glabella between the posterior part of the palpebral lobes, moderately convex; large low median tubercle close to anterior margin, row of 12 blunt spines evenly spaced along posterior edge. Occipital furrow with vertical anterior slope so that glabella adjacent to occipital ring stands higher than ring; glabella outlined by its convexity and by shallow axial furrows, expands forwards to maximum width (equal to that of occipital ring) opposite anterior part of palpebral lobe, is pinched-in opposite anterior end of palpebral lobe, then expands forward again to equal greatest width at margin of tongue. Latter is bounded laterally by narrow band of fixed cheek and deep axial furrow, there is no anterior cranidial spine; anterior edge of tongue with evenly curved outline and narrow preglabellar field laterally, which narrows almost to disappearance as mid-line is approached. Palpebral lobe with broad, gently convex rim which is widest posterolaterally and narrows forward; between rim and axial furrow is a small, crescentic flat area situated in the inner, anterior portion of the lobe. Free cheek like that of degree 0.

By the time the cranidium reaches a length (sag.) of about 1.24 mm. (Pl. 4, figs. 7, 8) the glabella has expanded between the palpebral lobes so that the earlier flat part of these lobes is eliminated, and the lateral margin of the glabella is separated from the palpebral rim by a palpebral furrow. This furrow is broadest at its mid-point, and in line with this point is the maximum glabellar width, which is greater than that of the tongue or the occipital ring. Beyond this size there is no major change in morphology of the cranidium. As size increases, convexity of the glabella increases, both longitudinally and transversely, and the axial-palpebral furrow becomes narrow and deep, with a vertical slope down from the glabella. Three pairs of muscle scars have been observed on glabella of cranidia of length (sag.) 2.5 mm. and upwards. Small tubercles occur on the external surface of the tongue and on the glabella adjacent to the palpebral furrow in cranidia of this same size, the raised lines appearing at a larger size. Free cheek that fits a cranidium of length (sag.) about 1.2 mm. (Pl. 4, figs. 11, 12) essentially like the largest, with narrow region outside eye lobe, doublure with pit, strong terrace lines and inner edge curled. Hypostomes of the smallest size known (Pl. 4, figs. 3, 4) fit a cranidium of length (sag.) 2.5 mm., and differ from the largest in that the spine on the posterolateral corner is longer.

Thorax and pygidium. Transitory pygidia from localities 3 and 4 are tentatively placed here. Tiny specimens of this type have not been recovered from localities 2, 6, or 15. Earliest in the presumed series are those having a length (sag., excluding spines) of 0.37 to 0.44 mm. (Pl. 4, figs. 5, 6, 13, 16-18, 22), and bearing a prominent upwardly-curving median axial spine of length almost 2 mm. The axis is convex, three-fifths the total width, not sharply bounded from the less steeply-sloping pleural regions. Three pairs of thornlike pleural spines are about equally spaced along the lateral and posterolateral margins, and between the last pair, on the posterior margin, there may be a tiny fourth pair (Pl. 4, fig. 5). The doublure is narrow and curled under, with a median posterior notch. The axis is crossed by broad, shallow ring furrows, the rings gently convex, and in front of the swollen base of the median spine there may be two rings (Pl. 4, figs. 5, 6, 13), one ring (Pl. 4, figs. 16-18), or none (Pl. 4, fig. 22). In all there is a shallow articulating furrow and an articulating half-ring. In those with the median spine at the anterior end of the axis, axial rings cannot be seen behind the base of the spine. In the holaspis (Pl. 2, fig. 12) the median axial spine is on the 4th segment in front of the pygidium, i.e.

the 8th thoracic segment if the total number is eleven. On this assumption the transitory pygidia with 2, 1 and no rings in front of the axial spine would be, respectively, those of degrees 5, 6, and 7. Specimens belonging to any one of these degrees vary in size within the limits mentioned. Those of degree 5 seem always to exhibit the fourth pair of pleural spines, but those of degrees 6 and 7 may, or may not, possess them. These transitory pygidia are similar to those described by Ross (1951, pp. 582-3, pl. 83, fig. 19; 1953, p. 634, pl. 62, fig. 20) as belonging to an older remopleuridid species.

The second group of transitory pygidia (Pl. 4, figs. 23-25) vary from 0.3 to 0.4 mm. in length (sag., excluding spines and articulating half-ring). The convex axis tapers backward and extends close to the posterior border. Up to four rings may be outlined by shallow ring furrows, the articulating furrow and anterior ring furrow being the deepest, those following being progressively shallower and the rings shorter (sag. and exs.). The third ring may show a faint median longitudinal depression, like those on the rings of the holaspid pygidium, and the fourth ring may be bilobate. Pleural regions narrow, less steeply sloping, lateral and posterolateral borders bearing triangular spines. These spines are differently developed on different specimens (probably corresponding to different degrees) — three pairs subequal in size and a tiny fourth posterior pair (Pl. 4, fig. 24), three subequal pairs (Pl. 4, fig. 25), or three pairs with the third small (Pl. 4, fig. 23). The doublure is curled under and bears the prominent terrace lines. Since these transitory pygidia bear no trace of the median axial spine, it seems likely that they belong to degrees 8-10, i.e. those succeeding the release of the spine bearing segment into the thorax. If they belonged to early degrees (1 to 4) they might be expected to show some sign of the median axial spine, unless this spine appears abruptly between moults. Further, the tip of the axis of the degree 0 transitory pygidium is strongly convex, quite unlike that of this type.

The smallest pygidia that are probably those of the holaspid (Pl. 4, fig. 21) are about 0.49 mm. in length (sag.), and are similar to larger specimens.

Remopleurides plaesiourus n.sp.

Plate 4, figures 26-30; Plate 5; Plate 6, figures 1-15.

Holotype. USNM 137677 (Pl. 5, figs. 3-5), locality 9.

Other Material. Paratypes USNM 137678a-e; all figured specimens in U.S. National Museum.

Geological Horizon and Localities. Lower Martinsburg shale, localities 9, 10, 12.

Description. This species is exceedingly like *R. caelatus* n.sp., differing from it in minor details of outlines, convexities, and proportions of parts of the exoskeleton. Comparisons between the photographs show that in *R. plaesiourus:*

a) glabellar tongue (compare Pl. 5, figs. 3, 4 with Pl. 1, figs. 3, 8) appears relatively narrower, is more inflated so that the slope down to the axial furrow is vertical, and the anterior area of fixed cheek is slightly wider. The preglabellar area dies out well before reaching the mid-line; in exterior view the outline of the anterior margin of the preglabellar area is almost straight, rather than obtusely angulate;

b) outline of palpebral rim in dorsal view (compare Pl. 5, fig. 5, with Pl. 1, fig. 5) is less curved in anterior half, more curved in posterior half, and the rim itself is wider (exs.) immediately in front of the occipital ring;

c) the different shape of the tongue and palpebral rim means that slight differences in shape are also present in the free cheek (compare Pl. 5, figs. 6, 7, with Pl. 1, figs. 4, 16) — in the outline of the inner margin of the eye surface and the course of the anterior branch of the suture. In addition, the librigenal spine is differently placed, and there is a deeper and wider notch between the base of the spine and the posterolateral part of the cheek;

d) the hypostome (compare Pl. 4, figs. 26, 29, 30 with Pl. 1, figs. 9-15) has a different outline, the anterior margin less strongly curved, the posterolateral part of the border slopes more steeply, the median boss is higher and sharper, the oval areas less inflated posteriorly;

e) the pygidium (compare Pl. 5, figs. 8, 9, 12-15 with Pl. 2, figs. 14-17, 19-21) shows the same kind of individual variation as that seen in *R. caelatus* in the relative length and amount of inflation of the inner pleural spine. Yet the inner pair of spines is relatively wider at the base and longer; the lateral margins of the pygidium are parallel-sided rather than backward converging and a low but distinct post-axial ridge is present, extending about half-way to the base of the notch between the inner pleural spines;

f) pattern of Bertillon lines on cranidium (compare Pl. 5, fig. 1 with Pl. 1, fig. 1) is different, and there are more granules in the mid-region of the median glabellar area. Median region of pygidium is also more granulate (compare Pl. 5, fig. 15 with Pl. 2, fig. 19).

Development. The development of *Remopleurides plaesiourus* is so like that of *R. caelatus* that much of the description given of the latter would apply to both species. The material of *R. plaesiourus* is less abundant and less complete in some respects. The protaspis (Pl. 5, figs. 18-20, 26) is broken at the anterolateral corners, so that the anterior cephalic spines are not seen. The protopygidium shows five axial rings, the fifth faint, in front of the convex tip of the axis, as do some broken specimens of *R. caelatus* (Pl. 3, fig. 6). In other respects the protaspides of the two species are alike.

The degree 0 cranidium of *R. plaesiourus* has slimmer anterior cephalic spines and the outline of the palpebral lobe is typical of this species in being more strongly curved posteriorly (compare Pl. 5, fig. 16, with Pl. 3, fig. 9). The transitory pygidium of degree 0 (Pl. 5, figs. 21-23) is like that of *R. caelatus*, and the few specimens show a small range in size.

A cranidium of length (sag.) 0.75 mm. (Pl. 6, fig. 1) shows a stage not found in the material of *R. caelatus* n.sp. It is very little larger than the degree 0 cranidium, the palpebral lobe has a faint rim, and the anterolateral margin continues the line of the anterior palpebral margin forward to meet the transverse anterior margin at an obtuse angle. Anterior cephalic spines are lacking, and the symmetrical form (three additional specimens are known from locality 10) suggests that the shape is not the result of breakage but of the inward shift of the anterior branch of the suture following the loss of the spine.

The next largest cranidium, of length (sag.) 0.79 mm. (Pl. 6, fig. 3) has the tongue with steeply sloping sides, and the anterior area of the free cheek. The glabella is narrowest in front of the occipital furrow and expands forward at an even rate to the maximum width at the anterior end of the tongue. The palpebral lobe has a well-developed rim, broadest posteriorly, and enclosed between the arc of the palpebral furrow and the straight axial furrow is a horizontal area. This area is larger than that in cranidia of the same size of *R. caelatus* (Pl. 4, figs. 1, 2) because in this latter specimen the glabella expands toward the mid-length of the eye lobes. The free cheek fitting the small cranidium of *R. plaesiourus* (Pl. 6, fig. 4) has the curve of the inner margin of the visual surface, and deep notch between base of spine and lateral margin, characteristic of this species (compare with that of *R. caelatus*, Pl. 3, fig. 16).

In the next two larger cranidia (Pl. 6, figs. 2, 5, 7, the original of fig. 5 of length (sag.) 1.27 mm.), the glabella bulges out between the eye lobes, and in larger cranidia (Pl. 6, figs. 8-12, 15) occupies the space between the palpebral furrows. From this size onwards there is little further change.

Transitory pygidia between degree 0 and probable degrees 8-10 are not known in *R. plaesiourus*, but those of degrees 8-10? (Pl. 5, figs. 24, 25) bear three pairs of marginal spines and are like those of *R. caelatus*.

Remopleurides caphyroides n. sp.

Plates 7-10; Plate 11, figures 1-4; Text-figure 6

Holotype. USNM 137681 (Pl. 7, figs. 1-3, 8, 10; Pl. 8, figs. 8, 10), locality 3.

Other Material. Paratypes USNM 137682a-e; all figured specimens in U. S. National Museum.

Geological Horizon and Localities. Edinburg formation, localities 2-6, 15. Fairly common at localities 2-4, rare at the others, especially at 6, where *R. caelatus* is common.

Description. All parts of the exoskeleton of this species may be differentiated from those of *Remopleurides caelatus* by the following characters:

(i) Glabella (compare Pl. 7, figs. 1-3 with Pl. 1, figs. 1-3, 5, 8) is more convex (sag. and tr.), especially anteriorly, and the relatively wider and more inflated tongue overhangs the anterior cephalic margin; palpebral rim is narrower in anterior part, and anterior area of fixed cheek is narrower. Outline of anterior edge of cranidium a curve, concave (rather than convex) ventrally. The two posterior glabellar furrows are faintly visible as curved, smooth strips, and the short anterior furrow is rarely visible (compare Pl. 7, figs. 3, 8 with Pl. 1, figs. 5, 6); all the furrows are less conspicuous than in *R. caelatus*. Posterior area of fixed cheek short (exs.) and narrow (tr.), the anterior margin a gentle "S" curve.

(ii) Free cheek (compare Pl. 7, figs. 1, 3-7, 9, 10 with Pl. 1, figs. 4, 10-12, 16) with anterior part of eye surface overhanging margin, external rim of eye lobe less conspicuous; doublure adjacent to median suture wider (sag. and exs.) and with more curved anterior margin; posterior margin outside suture curves gently forward to base of librigenal spine — there is no posteriorly directed projection outside the articulating socket, and the base of the librigenal spine is broader and the spine is differently directed. As in *R. caelatus* there is a pit in the doublure, appearing on the inner surface as a long, slim cone, the tip of which rests in a pit at the junction of the axial and preglabellar furrows (compare Pl. 8, figs. 8-10 with Pl. 2, figs. 23-25).

(iii) Hypostome (compare Pl. 7, figs. 4, 5, 7, 9 with Pl. 1, figs. 9-15) strikingly different, being transversely rectangular in outline with wider borders, prominent shoulder and posterolateral projection. Middle body separated from anterior border by shallow furrow, the oval areas with the long axis more widely divergent and enclosing a larger triangular area; on the anterior margin in the mid-line is a low rounded median boss. Anterior wing long and slim, no wing process, curving forward and upward so that distally it lies above the curled edge of the free cheek doublure. Posterior wing a large blunt projection.

(iv) Thoracic segments (compare Pl. 9, figs. 1-5, 7, 8, 12 with Pl. 2, figs. 1-13, 18, 19) have distal parts of axial rings only gently convex, less prominent axial articulating processes and sockets, longer (exs.) and wider (tr.) pleurae, flattened and tapering more gradually. The median spine on the eighth (?) thoracic segment is relatively slimmer and shorter.

(v) Pygidium (compare Pl. 9, figs. 6, 9-11, with Pl. 2, figs. 11-13, 18-21) lacks ring furrow defining median part of first axial ring, and pleural regions flattened, broadest at mid-length, bearing two pairs of border spines of which the outer are the longer.

(vi) External surface of glabella granulate in mid-part of median area (Pl. 7, fig. 3), with a row of larger granules along the posterior margin of the occipital ring in all but largest individuals (Pl. 8, figs. 1, 3, 5). Bertillon lines present on anterior and anterolateral parts of glabella (Pl. 7, figs. 1, 2) but not as conspicuous as in *R. caelatus*. On free cheek and hypostome, terrace lines run sub-parallel to margins. On axial rings of thorax, lines run transversely and there may be a row of granules along the posterior margin. On dorsal surface of pleural spines of thorax and pygidium each terrace line runs in a characteristic inverted "V" course (Pl. 9, figs. 3, 5, 6, 9, 12), and on the doublure the lines run sub-parallel to the lateral margins (Pl. 9, figs. 2, 4, 8, 11).

The cranidium, free cheek and hypostome have been associated by fitting together isolated specimens (Pl. 7; Pl. 8, fig. 7). The form of the occipital ring leads to association of the thoracic segments, and the pleurae of the latter may be matched in form and lines on external surface with pleural regions of the pygidium (Pl. 9, figs. 1-12).

Development

The supposed developmental series of *Remopleurides caphyroides* is illustrated in Plate 10 and Plate 11, figures 1-3. There is no complete size series of cranidia below a length of 1.7 mm. from any one locality. In this range, therefore, the series is tentative, being built up from specimens from different localities. The development of the cranidium will be described in descending order of size and the arguments given for the series here advocated. Cranidia of length (sag.) 2.5 mm. (Pl. 8, figs. 5, 6) (or larger) down to 1.73 mm. (Pl. 10, figs. 1-4) show a gradual transition — in the smallest example the glabella is relatively narrower, in longitudinal profile seen to be more convex and strongly arched at the base of the tongue, the anterior outline a rounded, inverted 'V' rather than a broad curve; the palpebral lobe is relatively wider (tr. and exs.), especially in the posterior part; external surface more coarsely granulate. A free cheek that approximately fits this cranidium is much like larger ones; smaller specimens are not known.

The next smallest cranidium comparable to the original of Plate 10, figures 1-4, is the original of Plate 10, figures 5-7, 0.92 mm. in length (sag.). The anterior part of the glabella has the same inverted 'V' outline in dorsal view and is more strongly raised, coming up to a blunt point in the mid-line at the base of the glabellar tongue; between the median part of the palpebral lobes the glabella is much narrower, the sides diverging forwards; a short basal glabellar furrow opposite the posterior part of the palpebral lobe, a longer median furrow opposite the middle part of the palpebral lobe — comparable positions to those of the

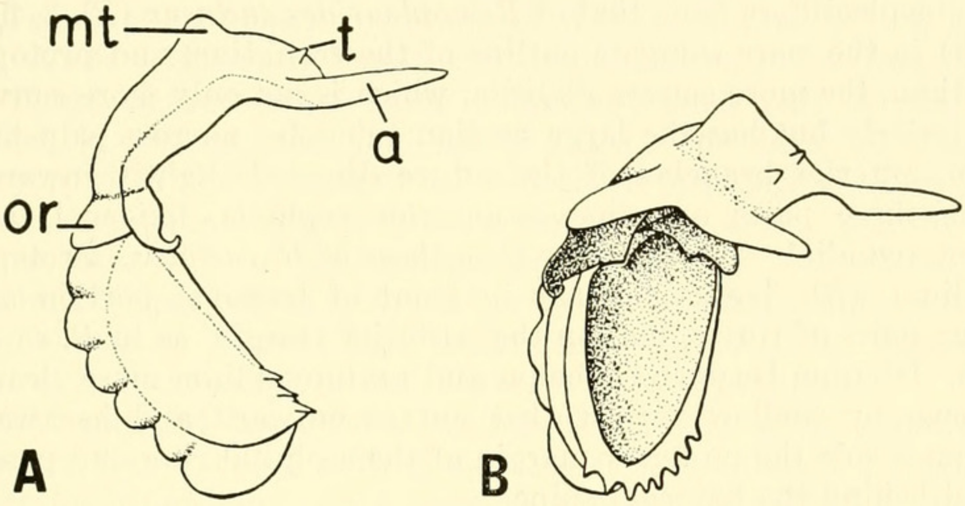


Figure 6. *Remopleurides caphyroides* n.sp. Outline reconstructions of degree 0 individual, lacking free cheeks and hypostome. A, right lateral, B, oblique views, X 30. Abbreviations: *a*, anterior cephalic spine; *mt*, median tubercle of glabella; *or*, occipital ring; *t*, tubercle. Based on originals of Plate 10, figures 8-14, 16, 17.

furrows in larger glabellae. The palpebral lobe is subsemicircular in outine, horizontal, and with a faint rim.

It seems reasonable to suggest that the preceding stage of the cranidium (believed to be degree 0 by analogy with *R. caelatus*) is that shown in Plate 10, figures 8-11, 13 (cf. Text-fig. 6) with the striking large median glabellar tubercle situated opposite the anterior end of the palpebral lobes. The occipital ring is relatively narrow, the glabella straight-sided and expanding forward; two pairs of smooth areas are the lateral glabellar furrows, situated in the same relative position as in the next larger cranidium; about mid-way down the anterior slope is a pair of tiny tubercles. Anterior cephalic spines are long and curved, and there is a slight swelling at the tip of the posterior area of the fixed cheek suggesting a fixigenal spine; palpebral lobe gently convex and outward sloping, narrow rim. External surface granulate, prominent median occipital tubercle.

The protaspis preceding this degree 0 cranidium can hardly be other than that shown in Plate 10, figures 15, 18-20, and Plate 11, figures 1-4, the cranidium differing in its greater longitudinal convexity, and in exhibiting slim fixigenal spines. This protaspis differs from that of *Remopleurides caelatus* (Pl. 3, figs. 1-5) in the more elongate outline of the cranidium and protopygidium, the more convex glabella, which is not only more convex anteriorly but has the large median tubercle; narrow palpebral rim, anterior branches of the suture directed slightly inwards. The three pairs of spines — anterior cephalic, fixigenal, and protopygidial — are slimmer than those of *R. caelatus*. Protopygidium with five axial rings in front of terminal portion and four pairs of tiny spines on the posterior margin, as in *R. caelatus*. Division between cephalon and protopygidium more clearly shown by shallow furrow that curves outward and backward from beside the posterior margin of the occipital ring and passes just behind the fixigenal spine.

The degree 0 cranidium of *R. caphyroides* (Pl. 10, figs. 8-11, 13) is also distinguished from that of *R. caelatus* (Pl. 3, figs. 7, 9) by the outline, median glabellar tubercle, narrow palpebral rim, and slimmer anterior cephalic spines. The degree 0 transitory pygidium here referred to *R. caphyroides* (Pl. 10, figs. 12, 14, 16, 17) is extremely like that of *R. caelatus* (Pl. 3, figs. 8, 10-15), differing in being larger and relatively longer, the outline being suboval rather than subcircular. These two transitory pygidia occur together at localities 2, 3, and 4, but can be separated by size (though each type shows some range in size) and outline, especially at locality 2 where both species are common. At locality 6, where *R. caphyroides* is extremely rare, the transitory pygidia are all of *R. caelatus* type. It may be added that the degree 0 transitory pygidium of *R. plaesiourus* (Pl. 5, figs. 21-23) is of the same size and outline as that of the closely related *R. caelatus*.

Comparison between the protaspides of *R. caphyroides* (Pl. 10, figs. 15, 18-20; Pl. 11, figs. 1-3) and *R. caelatus* (Pl. 3, figs. 1-6) shows that the outlines and size of the protopygidia differ in the same way as do the degree 0 transitory pygidia. The degree 0 transitory pygidium of *R. caelatus* is smaller than the protopygidium of the protaspis of *R. caphyroides*, whereas the degree 0 transitory pygidium referred to *R. caphyroides* is larger.

Small hypostomes of *R. caphyroides* (Pl. 9, figs. 16, 17) differ from the largest in the more square outline, greater convexity of the middle body, the presence of a blunt median spine (rather than boss) and a spine at the posterolateral angle.

The smallest known pygidium of *R. caphyroides* (Pl. 9, figs. 18, 22) is 0.52 mm. in length and does not seem to be transitory — it differs from larger ones in that the inner pair of pleural spines is close together and partly fused. The degree 0 transitory pygidia of *R. caphyroides* and *R. caelatus* are similar, but there seems no reason to believe that the transitory pygidia of *R. caelatus* with the long median axial spine (Pl. 4, figs. 5, 6, 13, 16-18, 22) may belong to *R. caphyroides* — the latter species does not have such a prominent median axial spine in the holaspid thorax and the shape of the pleural regions is different.

The material described above has been found at the following localities: protaspis, localities 2-5; degree 0, localities 2, 3 (transitory pygidium only), 4, 6, and 15 (cranidium only); parts of larger exoskeletons are relatively abundant at localities 2 and 3, few at localities 4, 6, and 15, and unknown from 5. From localities 3 and 4 come cranidia of length (sag.) 1.3 mm. (Pl. 11, figs. 5-8) which in size and other characters are intermediate between the originals of Plate 10, figures 1-4 and 5-7 — in outline of glabella between palpebral lobes, in form of lateral glabellar furrows, and size of papebral lobe. The anterior part of the glabella, however, has a broadly rounded outline in dorsal aspect, and in lateral aspect lacks the sharp convexity. Further, and also only from localities 3 and 4, comes a degree 0 cranidium (Pl. 11, figs. 9-11) like the original of Plate 10, figures 8-11, 13, except that it lacks the large, rounded median tubercle on the anterior part of the glabella. No protaspis of this type is known. Two possible explanations occur for these cranidia: (a) they are part of the developmental series of an otherwise unknown species of

Remopleurides, or (b) they are part of the *R. caphyroides* developmental series. Acceptance of the latter alternative would mean that in the early meraspid development of the cranidium of some individuals the median glabellar tubercle was abruptly reduced between protaspis and degree 0 and the glabellar tongue consequently rounded in dorsal outline. I know of no comparable case of morphological differences between groups of early meraspides of a single species.

Remopleurides asperulus n.sp.

Plates 12, 13.

Holotype. USNM 137683 (Pl. 12, figs. 1, 2, 4, 6, 14), locality 13.

Other Material. Paratypes USNM 137684 a-c; all figured specimens in U. S. National Museum.

Geological Horizon and Localities. Upper Lincolnshire limestone, localities 1a, 13.

Description. This species is the only remopleuridid in the upper Lincolnshire limestone, and the first to appear in the Middle Ordovician of the Shenandoah valley. The silicification is relatively coarse-grained, and the surfaces of most of the specimens have granules (probably of quartz) adhering to them or growing out of them. A fairly complete growth series is known.

Cranidium (Pl. 12, figs. 1, 2, 4, 6, 14) wider than long, maximum width at the mid-length, the margin of the palpebral lobe projecting farther out than the tip of the posterior area of the fixed cheek. Free cheek (Pl. 12, figs. 3, 5, 11, 20) correspondingly narrow, the convex eye surface overhanging the margin antero-laterally, the postero-lateral portion, outside the external rim of the eye lobe, narrow, triangular, steeply sloping, with a blunt, short librigenal spine. Occipital ring moderately convex, longest (sag.) in the mid-line, deep, narrow occipital furrow. Remainder of glabella evenly and moderately convex (tr. and sag.), outlined by narrow palpebral and axial furrows; glabellar tongue two-fifths maximum width of cranidium, bent down steeply to overhang slightly anterior margin of cephalon. Glabellar furrows visible on inner surface as grooves (Pl. 12, fig. 14), basal furrow long, curved, opposite greatest width of glabella, second furrow shorter, curved, opposite a point about one-third length of palpebral lobe. Palpebral lobe widest posteriorly, narrowing progressively forward and continuous with extremely narrow anterior area of fixed cheek. Doublure of cephalon widest anteriorly; beside median suture a narrow posterior portion is flexed up vertically and then bent back horizontally (Pl. 12, fig. 3) — this flexure dying out rapidly away from the median suture; anterolaterally doublure curled up at inner edge, and extending back to where the suture cuts posterior cephalic margin. Pit in doublure (Pl. 12, fig. 11) appearing as a long, slim cone on inner surface (Pl. 12, fig. 3); tip of cone lies close to anterior pit. Hypostome (Pl. 12, figs. 7, 8, 12) subrectangular in outline, wider than long, middle body with prominent median boss and diagonally directed oval areas; borders broad, blunt spine at posterolateral angle, anterior wing short, posterior wing small.

Thorax of at least nine segments (Pl. 12, figs. 15-18). Axis broad, two-thirds width of segments, pleurae steeply sloping, with short pleural spines except for long spine on fifth segment from posterior. Short, blunt median axial spine on fourth segment from posterior. Prominent axial articulating processes and sockets. Doublure extends in to axial furrow, posterior part crossed by a sharp, curving and transversely directed flexure which borders a depressed (in ventral view) posterior area that receives the anterior part of the succeeding segment during enrollment (see Pl. 12, fig. 17, anterior segments on left side). Pygidium (Pl. 12, figs. 15-18) wider than long, broad, short axis tapers rapidly to rounded termination, first axial ring narrow (sag.) medially and expanding laterally into a lobate area, second axial ring bilobate and lying between outer parts of first ring. Steeply sloping pleural regions having two pairs of short, blunt, posteriorly directed spines, deep notch between inner pair, smaller notch between the pairs. Doublure broad, bent upwards, median posterior projection.

External surface bearing anastomosing terrace lines — on cheek (Pl. 12, fig. 20) running sub-parallel to margins, on thorax and pygidium (Pl. 12, fig. 15) transversely on axis, on pleurae curving distally to run subparallel to long axis. Along posterior margin of axial rings a row of low tubercles, largest laterally. On doublure (Pl. 12, figs. 11, 17) terrace lines strong and everywhere subparallel to inner margin; on hypostome lines run diagonally on middle body, and along the borders.

Development

Protaspis (Pl. 13, figs. 1-4, 10). Subspherical in shape, convex cranidium with protopygidium curled closely beneath it. Owing to the coarse grain of the replacement, details cannot be observed. The axis is not defined. In lateral view scalloped lateral margin of cranidium shows position of palpebral lobe and course of anterior branch of suture. A second incomplete specimen (not illustrated) shows four pairs of tiny spines along the curled posterior margin of the protopygidium, and a larger pair of spines on the steep flanks in front of the outermost marginal pair. Anterior cephalic spines are either absent or not preserved. What may be the fixigenal spine is visible a short distance inward and backward from the base of the palpebral lobe.

Degree 0 (Pl. 13, figs. 5-7). Cranidium believed to be this degree, of length 0.83 mm., gently convex transversely, strongly convex longitudinally so that short (sag.) glabellar tongue descends vertically. Maximum width of cranidium at about half length and almost same as length (sag.), palpebral margin projects out farther than posterior area of fixed cheek. Occipital ring is well-defined, convex, width about one-third that of cranidium, with median tubercle, and in front of it axial furrows extend directly forward a short distance, outlining the gently convex posterior part of the glabella, and then die out. One specimen (not illustrated) suggests that a short anterior cephalic spine is present; fixigenal spine absent. External surface granulate.

Transitory pygidium (Pl. 13, figs. 11-15) of length ca. 0.9 mm., maximum width four-fifths of length; at three-quarters the length high and strongly convex so that lateral and posterior slopes are vertical, maximum convexity and height at point of greatest width. Axis about one-third total width, with prominent articulating half ring; six gently convex rings progressively shorter (sag.) posteriorly, and a more convex semi-cylindrical posterior portion situated on the posterior slope. Each ring is separated from the others and the posterior portion by a faint ring furrow, and there is a stronger articulating furrow, but axial furrows as such are not present. Doublure is present around postero-lateral margins, curled under, and along the curled edge is a curving row of 5 spines, the innermost pair close together on the ventrally-facing surface of the doublure immediately behind the tip of the axis, the other spines evenly spaced along the pleural margins. External surface finely granulate, the granules present on the axial rings but not in the furrows. On the posterior parts of the pleural regions curving granulated bands, separated by narrow smooth bands (Pl. 13, fig. 14), run out from the last 3 rings to the pleural margin. Each of these bands ends against the base of a marginal spine, and the second, third and fourth pairs seem thus to belong to the three axial rings in front of the terminal axial portion.

Further Development. The next smallest cephalon (Pl. 13, fig. 17), cranidium of length (sag.) 1.0 mm., has the axial furrow visible as a change in slope between glabella and palpebral lobe, extending forward from the margin of the occipital ring to the edge of the tongue in a curve gently convex outward. Glabellar tongue is curved gently downward, width about half maximum width of cranidium. Palpebral lobe is gently convex, rim distinct and widest posteriorly. Free cheek with long, slim librigenal spine. At the next size known (Pl. 13, figs. 20-22, cranidium of length 1.4 mm.) the glabella extends between the palpebral furrows and is gently and evenly convex transversely. Width (tr.) of tongue is more than half maximum width of cranidium. As size of cephalon increases (Pl. 13, figs. 23-31), the major changes that take place are relative increase in maximum width of cranidium so that it becomes greater than length, and this is accompanied by increase in curvature of the palpebral rim in dorsal view, and steeper down-bending of glabellar tongue so that the tongue becomes barely visible in dorsal view. The librigenal spine is progressively reduced to a blunt, short point. Granulation on the external surface becomes relatively finer, and can scarcely be seen in the larger specimens, partly owing to the preservation. Glabellar furrows are faint or invisible in most specimens, an exception being the original of Plate 13, figures 24-26, in which the furrows are represented by shallow grooves in the external surface.

Smallest hypostome known (Pl. 13, figs. 8, 9) differs from largest principally in having a longer posterolateral spine.

An example of the transitory pygidium (Pl. 13, figs. 16, 18, 19) probably belongs to the later degrees of the meraspid period.

The first ring of the broad axis is continuous with the posteriorly directed spinose pleura, and the articulating half ring and process is typical. Behind and inside this segment the next ring is demarcated, and there are two pairs of pleural spines; between the median pair of spines is the deep notch characteristic of the holaspis.

REMOPLEURIDES EXIMIUS n.sp.

Plates 14, 15, 16.

Holotype. USNM 137685 (Pl. 14; Pl. 15, fig. 1), locality 4.

Other Material. Paratypes, USNM 137686a, b; all figured specimens in U. S. National Museum.

Geological Horizon and Locality. Lower Edinburg limestone, localities 3 and 4. One specimen of the degree 0 transitory pygidium attributed to this species comes from locality 2.

Description. The holotype specimen is an exceptionally complete exoskeleton lacking only the right free cheek and the hypostome. Only a few other exoskeletal parts come from locality 4, but these include the hypostome. At locality 3 this species is less common than *Remopleurides caphyroides* n.sp. and about as abundant as *R. simulus* n.sp. *R. eximius* n.sp. resembles closely *R. asperulus* n.sp. from the Upper Lincolnshire limestone, and it is largely because of this similarity that a hypostome occurring at localities 3 and 4 has been attributed to it. *R. eximius* may be distinguished from *R. asperulus* by the following characters: —

Glabellar tongue (compare Pl. 15, fig. 1 with Pl. 12, fig. 4) of width (tr.) about half that of glabella, palpebral rim narrower posteriorly and outline in dorsal aspect evenly curved rather than a markedly stronger curvature in the posterior part. Free cheek extremely similar, but having a different curvature of the eye lobe and a more marked depressed region in the posterior part of the doublure. This depressed region receives the facet of anterior thoracic pleura during enrollment (Pl. 14, fig. 2). Hypostome (compare Pl. 15, figs. 2, 4, 10 with Pl. 12, figs. 7, 8, 12) differs from that of *R. asperulus* in details of outline and in having a larger shoulder.

Thorax (Pl. 14; Pl. 15, figs. 6-8, 11, 12) of 11 segments, a longer pleural spine on the seventh and a median axial spine on the eighth. Pygidium (compare Pl. 15, figs. 9, 13, 14 with Pl. 12, figs. 15, 16, 18) distinguished by the convexity of the axis and consequent depth of furrows, including the median longitudinal; posterior notch between inner pair of pleural spines broader.

Development of *Remopleurides eximius* n.sp. ?

Protaspis. A distinctive protaspis (Pl. 16, figs. 1-7, 9), quite abundant at locality 3 but also present at locality 4, has been attributed to this species because of its resemblance to that of *Remopleurides asperulus* n.sp. This protaspis is far better preserved than that of *R. asperulus,* though in neither case is the free cheek or hypostome known. Cranidial portion evenly convex (sag. and tr.), the occipital ring (Pl. 16, fig. 2) faintly outlined by both occipital and axial furrows and width of about one-third that of the cranidial portion. Conspicuous pair of tubercles close to mid-line and situated near anterior margin of the glabellar tongue (Pl. 16, figs. 4, 6). Margin of palpebral lobe with narrow rim, branches of suture distinct. Curving outward and backward from occipital furrow is a faint change in slope, the posterior border furrow (Pl. 16, fig. 2). Subparallel to this furrow and running out from the posterior margin of the occipital ring is a faint furrow that marks the boundary between the cranidial and protopygidial portions (Pl. 16, fig. 7). Short slim anterior cephalic spine, and the fixigenal spine of similar size; the latter situated close to the cranidial margin and at about half the width of the posterior border. Protopygidium strongly convex (sag. and tr.), especially posteriorly. At the curled posterolateral margin may be seen four pairs of tiny spines, a fifth, outer and larger anterior pair situated slightly farther inside the margin (Pl. 16, fig. 6); these five pairs about equi-distant from each other. Segmentation of the protopygidium is revealed by the transverse bands alternately finely granulate and smooth (Pl. 16, figs. 7, 9). These bands run subparallel to the faint furrow which separates cranidium and protopygidium and curve downwards and backwards over the steep sides. At least five bands can be distinguished following the occipital ring, but separate bands cannot be made out on the vertical lateral portion. Axis extremely faintly outlined in the first two of these bands following the occipital ring. The doublure is relatively broad and curled under, extending laterally as far as the posterior edge of the cranidial portion.

Degree 0. Both the cranidium (Pl. 16, figs. 8, 10-12) and transitory pygidium (Pl. 16, figs. 13-17) are relatively abundant at localities 3 and 4 and are like those of *R. asperulus* (Pl. 13, figs. 5-7, 11-15), notably in the distinctive form of the transitory pygidium. Occipital ring of cranidium convex, with median tubercle, occipital furrow deep, continued across fixed cheek by deep posterior border furrow. Glabella convex (sag. and tr.), tongue bent down vertically, anterior cephalic spine at anterolateral corner long and slim. Two pairs of lateral glabellar furrows visible (Pl. 16, fig. 10) in posteromedian part of glabella as smooth ovate areas; the anterior furrow directed diagonally inward, the posterior directed diagonally inward and forward. In anteromedian part of glabella is a narrow, sagittal, smooth band which dies out at base of tongue. Pair of tubercles close to mid-line of tongue (Pl. 16, fig. 8). No fixigenal spine on posterior border. Transitory pygidium with large articulating half ring. Along posterior margin 5 pairs of short spines arranged in a curving line (Pl. 16, fig. 17). Segmentation in the transitory pygidium again indicated by alternate granulate and smooth bands which curve downward and backward over the steeply sloping lateral portions. Six granulate bands may be recognized (Pl. 16, fig. 13), separated by five smoother bands, and on the vertical slope behind the sixth band may be seen (Pl. 16, fig. 16) a long narrow convexity representing the posterior part of the axis.

Developmental stages intermediate between those of this degree 0 and the supposed holaspis are not known. The degree 0 cranidium (Pl. 16, figs. 8, 10-12) is quite different in outline and convexity from that (Pl. 11, figs. 9-11) here placed in *R. caphyroides?*

Remopleurides simulus n.sp.

Plate 17; Plate 19, figures 11, 12.

Holotype. USNM 137687 (Pl. 17, figs. 1, 2, 4, 5), locality 3.

Other Material. Paratypes USNM 137688a-c; all figured material in U. S. National Museum.

Geological Horizon and Locality. Lower part of Edinburg limestone, locality 3.

Description. This species, the fourth to be described from locality 3, does not resemble closely either *Remopleurides caelatus* or *R. caphyroides*, but differs from *R. eximius* in the following minor characters (these characters also serve to distinguish this species from *R. asperulus*, which occurs at a lower horizon):

Glabella with relatively slightly wider tongue (compare Pl. 17, fig. 1, with Pl. 15, fig. 1); the glabella and tongue are gently convex (sag. and tr.), the longitudinal convexity less than that in *R. eximius* (compare Pl. 17, fig. 2 with Pl. 14 fig. 3). Outline of palpebral rim gently curved, only slightly curved in posterior half, free cheek with slim librigenal spine situated in advance of the genal angle, the base being about opposite the posterior part of the eye lobe. Hypostome (compare Pl. 17, fig. 18 with Pl. 15, fig. 2) with strong curve to anterior margin, posterolateral corner angulate but not drawn out into a spine. Thorax (compare Pl. 17, fig. 11 with Pl. 15, fig. 7) distinguished by the flattened appearance of the axial rings, the tuberculation on the posterolateral margin being fine; pleurae likewise flattened, bladelike, the posterolateral corner extended into a blunt, backwardly-directed spine. The fifth thoracic segment from the posterior (probably the seventh segment) does not have elongated pleurae but the succeeding segment (probably the eighth) has a slim median axial spine. Pygidium (compare Pl. 17, figs. 11, 19 with Pl. 15, figs. 9, 13) with less inflated axis and consequent shallower furrows. Articulating process outside axial furrow prominent. Two pairs of pleural spines on posterior margin equally spaced from each other and without a markedly deeper median notch between the inner pair.

It may be argued that the exoskeletons included here under *R. simulus* may be sexual dimorphs of those exoskeletons included under *R. eximius*. An admittedly inconclusive argument against this view is that *R. simulus* does not occur at locality 4, where *R. eximius* is present. While localities 3 and 4 are not far apart geographically there may be a slight difference in horizon between them, as exemplified by the species peculiar to each locality (see lists above).

No early developmental stages of this species are known.

Remopleurides rugicostatus Raymond (1925, p. 57, pl. 3, fig. 3; this paper, Pl. 18, figs. 23, 24, 26, 27), from the Ridley limestone

(Wilderness stage) of Tennessee, is based on a single, incomplete, enrolled exoskeleton that probably has the outer exoskeletal layers missing. The cranidium and anterior thoracic segments are like those of *R. simulus*, and on the anterior pleural band of both species raised lines run in convex curves forward and outward from the pleural furrow. The pleura of the seventh segment does not appear to be elongated in *R. rugicostatus;* the axial ring of the eighth segment is broken. Free cheek, hypostome and pygidium are unknown in *R. rugicostatus*, and because of this lack of knowledge a new name is given to the Virginia material; clearly *R. rugicostatus* and *R. simulus* are closely related, the former being slightly the younger (Cooper, 1956, Chart I).

Genus ROBERGIA Wiman, 1905

ROBERGIA MAJOR Raymond, 1920

Plate 18, figures 1-22, 25.

Material, Localities and Geological Horizon. Lower part of Edinburg limestone (Liberty Hall facies), locality 14, a few cranidia and hypostomes from locality 16.

Description. This species was illustrated by Raymond (1925, pp. 60-61, pl. 3, figs. 6-10) and later redescribed by Cooper (1953, pp. 22-23, pl. 8, figs. 7-11). At the same time Cooper (1953, p. 22, pl. 12, figs. 10-14) redescribed the species *Robergia athenia* Butts, 1926, and some of the material he illustrated came from the present locality 14. Cooper stated (1953, p. 22) that *R. athenia* "differs from *R. major* chiefly in the shorter, more expanded frontal lobe of the glabella, by possessing a broad untapered axial lobe on the thorax, and by having the middle pair rather than the outer pair of pygidial spines longer than the other two." I consider the first two of these distinctions of doubtful value, and a re-examination of the type material of *R. major* shows that the pygidium bears three pairs of pleural spines, the outer pair extremely small and short, the middle pair the longest, the inner pair short and close together near the midline. The pygidium of *R. athenia* appears to be extremely similar and I therefore regard these two species as one, and they come from approximately the same horizon.

In redescribing the type species of *Robergia* (Whittington, 1950b, pp. 543-544, pl. 71, figs. 1-8), I pointed out that the hypostome was not known from the Swedish specimens. Raymond described the hypostome of *R. major* as bifurcated. The original material includes one specimen marked by Raymond as being the hypostome, but this specimen is a poorly preserved external mould of a pygidium. At locality 14 *R. major* is the most abundant of two remopleuridids that are present, and the hypostome described below is thought to belong to it.

Cranidium typical of *Robergia*, the glabella having 3 pairs of lateral glabellar furrows, the middle pair the longest and the most strongly curved. The basal glabellar lobe (Pl. 18, figs. 3, 5), situated adjacent to the inner end of the eye lobe, is subcircular in outline and has a faint independent convexity. Palpebral rim continuous with narrow anterior area of fixed cheek and preglabellar area (Pl. 18, figs. 3, 4, 7). Free cheek (Pl. 18, fig. 2) subtriangular in outline, a narrow convex border, the base of the genal spine situated opposite the midpoint of the eye lobe, the spine long and slim. Eye surface (Pl. 18, fig. 18) with many tiny facets arranged in diagonal lines. Doublure narrow, crossed anteriorly by a median suture. Hypostome (Pl. 18, figs. 8-14) subsquare in outline, anterior border flattened and continuous laterally with the large anterior wing. Lateral and posterior borders narrow, convex, separated from the middle body by deep furrow, small shoulder, spine at posterolateral angle. Middle body bearing the characteristic pair of gently convex ovate areas; anteriorly these areas separated by a triangular depressed area, this depression interrupted by the median boss; posteriorly the oval areas separated only by a shallow furrow. Doublure narrow, small posterior wing.

Pygidium (Pl. 18, figs. 15, 19, 22, 25) subrectangular in outline, slightly wider than long. Axis at anterior margin one-third of width, tapering evenly back to reach about four-fifths of the length and continued to the posterior margin by a narrow postaxial ridge. Some five axial rings may be distinguished. Pleural regions horizontal, the outer pair of pleural spines situated on the lateral margin at about three-quarters the length, the middle and largest pair at the posterolateral corner, and the third pair close together near the midline. First two interpleural ridges curve back to reach the posterior margin of the corresponding spine; third pair of interpleural ribs faint and close to the post-axial ridge. Doublure broad, inner margin reaching a line joining the anterolateral corner to the posterior tip of the axis.

The specimens are not well preserved, being somewhat flattened and distorted. Details of the external surface cannot be discerned except for the fine subparallel lines on the oval areas of the hypostome.

Development. Small specimens of only the cranidium are known, the smallest being of length (sag.) 1.2 mm. (Pl. 18, fig. 16). Glabella clavate in outline, the occipital ring narrow (sag.), convex, defined by a deep occipital furrow; the shallow axial furrows diverge forward to the maximum width opposite the anterior end of the eye lobes; in front of this point the glabella narrows slightly and is rounded. Three pairs of lateral glabellar furrows appear as short broad depressions, their positions being about as in larger cranidia, the posterior pair reaching the axial furrow, the anterior pair commencing inside the axial furrow and the shortest. Palpebral rim broad, convex, defined by a shallow furrow which runs anteriorly into the axial furrow. Anterior branches of the facial suture diverge forwards, then opposite the anterior end of the glabella curve around and run strongly inwards to meet the midpoint. A semicircular horizontal portion of the fixed cheek is thus enclosed between the palpebral rim and the axial furrow, and a further section of the fixed cheek and preglabellar area is enclosed between the anterior branches of the suture.

The next largest cranidium (Pl. 18, figs. 17, 20, 21) is of length (sag.) 1.88 mm. The glabella is now relatively broader and expands between the eye lobes so that only a narrow crescentic depression separates the glabella from the palpebral rim. In position and length the lateral glabellar furrows are much as in the largest cranidia and the basal lateral lobes display the subcircular outline and gentle convexity. The anterior part of the glabella, however, does not expand in front of the eye lobes but narrows slightly so that outside the axial furrows there is still a relatively broad portion of the fixed cheek. The preglabellar area appears relatively shorter (sag. and exs.). The free cheek that fits this size of cranidium is similar in form to that of the largest specimens known. The next largest cranidium known (Pl. 18, fig. 4) is approximately 4 mm. in length (sag.). Evidently during development to this size the glabella expands between the eye lobes so that the lateral margin is adjacent to the palpebral rim, and also expands in front of the eye lobes so that the anterior area of the fixed cheek becomes narrower.

The small pygidium (Pl. 18, figs. 15, 19), of length 1.5 mm., (sag.) is from locality 16 and is not distorted. It shows clearly the form of the pleural spines, in particular of the outermost pair.

Discussion of Development. Small cranidia of *R. major* (Pl. 18, figs. 16, 17, 20, 21) are like those of *Menoparia* (Ross, 1951, pl. 81, fig. 14; 1953, pl. 62, fig. 3) in width (tr.) of the anterior area of the fixed cheek and shape of the preglabellar area. *Robergia* may therefore be more closely related to *Menoparia* than to *Remopleurides.* In the development of the cranidium of *Robergia* the same major features are shown as in the development of *Remopleurides* — the expansion of the glabella between the palpebral rims and the reduction in width of the anterior area of the fixed cheek and the preglabellar area.

ROBERGIELLA n. gen.

Type species. Robergiella sagittalis n. gen., n. sp.

Discussion. The material included here occurs with *Robergia major* at locality 14, and with *Remopleurides caelatus* at locality 16, and displays holaspid characters that are intermediate between them. The cranidium has rather the form and outline of *Remopleurides,* the eye lobe being relatively long and the palpebral rim broad; the glabellar tongue expands forward, but apparently not as strongly as in typical *Robergia.* The three pairs of lateral glabellar furrows, however, are like those of *Robergia,* yet the basal glabellar lobe is not subcircular and slightly inflated. The free cheek is relatively broad with a narrow border and doublure, base of the genal spine being opposite the occipital ring. The thoracic segments lack the large axial articulating processes and sockets typical of *Remopleurides* and have the inner part of the pleurae crossed by a broad shallow pleural furrow as in typical *Robergia.* Axis of the pygidium includes only two pleural rings, the second divided by a median longitudinal furrow as in *Remopleurides,* and there is a post-axial ridge. Pleural regions are flattened, bordered by two pairs of long, tapering spines directed backwards, a strong interpleural ridge separating the proximal parts of the pleurae.

ROBERGIELLA SAGITTALIS n. gen., n. sp.

Plate 6, figures 16-33.

Holotype. USNM 137679 (Pl. 6, figs. 16, 17), locality 14.

Other Material. Paratype USNM 137680, all figured material in U. S. National Museum.

Geological Horizon and Localities. Lower part of the Edinburg limestone, Liberty Hall facies, localities 14, 14a and 16.

Description. Occipital ring longest in the midline, tapering distally to a blunt point at the axial furrow, the distal portion lying immediately behind the posterior part of the eye lobe. Median tubercle lies at the anterior margin. In front of the deep, narrow, occipital furrow, width of the glabella (Pl. 6, figs. 16-18) about the same as that of the base of the tongue; immediately in front of this basal portion the glabella expands between the palpebral rims. The tongue of length (sag.) less than half that of the eye lobe and curved only gently downward; narrow anterior area of fixed cheek. Three pairs of narrow, deep, lateral glabellar furrows, equally spaced from each other and from the occipital furrow, the anterior pair opposite the anterior part of the eye lobe; the furrows are diagonally directed, the first and second the longest, slightly curved, the third short.

Eye lobe moderately curved, convex palpebral rim defined by deep palpebral furrow; eye surface vertical with many tiny facets (Pl. 6, fig. 33), narrow convex external rim. Anterior branch of facial suture (Pl. 6, fig. 26) has a forward and outwardly directed course immediately in front of eye lobe; posterior branch of the suture (Pl. 6, fig. 16) directed strongly outwards across the posterior border so that it reaches margin at a point about two-thirds of the width of the cheek (tr.). Free cheek (Pl. 6, figs. 16, 17, 27) subtriangular in outline, greatest width along the line of the posterior border furrow, which is directed transversely. Anterolateral and lateral border narrow, convex, defined by a deep border furrow; at the genal angle the lateral border is continuous with the long slim genal spine. Posterior border slightly wider (exs.), small notch in the margin immediately inside the base of the librigenal spine. Doublure (Pl. 6, fig. 23) rolled beneath the border and not extending in beyond the lateral and posterior border furrows.

Three incomplete thoracic segments are known, one of which is attached to the holotype (Pl. 6, figs. 16, 17, 19, 24). Axial ring convex, inner part of pleura horizontal, transversely directed, and crossed by a deep diagonal pleural furrow; adjacent to the axial furrow the pleural furrow is subdivided by a low swelling, subtriangular in shape, which extends a short distance distally. Outer part of pleura curved, flattened, and pointed, the pleural furrow extending onto this portion and becoming shallower distally. One segment with long median axial spine.

Pygidium (Pl. 6, figs. 29-32) with convex axis tapering rapidly backwards, extending to about two-thirds the length (sag.), postaxial ridge becoming narrower posteriorly but reaching the margin. Axis with deep articulating furrow and subdivided into two rings by the shallow axial furrow; posterior of the two rings subdivided into two subcircular lobes by a median longitudinal furrow. Pleural regions horizontal, divided by an interpleural ridge which runs backward and slightly outward from the ring furrow, and by the postaxial ridge. Shallow pleural furrow curves outward and backward on the anterior segment, and adjacent to the axial furrow is subdivided by the low swelling. Each pleura continued by a backwardly directed gently tapering spine. Doublure broad, extending inward to tip of axis.

External surface bearing fine, raised, anastomosing lines, these lines running transversely on the occipital and axial rings, in curves convex forward on the outer parts of the pleurae of thorax and pygidium. On the free cheek between the eye lobe and the border furrows the raised lines form a reticulate pattern (Pl. 6, fig. 27). A row of small tubercles along the posterior margin of the occipital and axial rings. On the median axial spine of the thorax and the doublure, raised lines run longitudinally, subparallel to the margins.

Discussion. This species is not common at any of the localities at which it occurs, and the hypostome is not certainly known. A few small cranidia occur at locality 19 (Pl. 6, figs. 20-22) which may belong to this species. The example figured, of length (sag.) 2.13 mm., shows the three pairs of glabellar furrows (the anterior pair faint), and the palpebral rim is relatively wider than in larger individuals. This specimen is referred to below in connection with the indeterminable small remopleuridid.

Remopleuridid gen. et sp. ind.

Plate 19, figures 1-10.

Material. Figured specimens, USNM 137689a-f.

Geological Horizon and Localities. Lower Edinburg limestone, localities 3 and 4.

Description. This cephalon occurs with *Remopleurides caelatus, R. caphyroides, R. eximius,* and *R. simulus,* and the largest cranidium known (Pl. 19, fig. 9) is only of length (sag.) 1.84 mm. It most closely resembles that of *R. caelatus* but differs from those of comparable size of this species (and of the other species mentioned). From *R. caelatus* (Pl. 3, fig. 16; Pl. 4, fig. 14) it is distinguished by the wider (especially posterolaterally) palpebral rim and the wider (tr.), more rapidly expanding and less steeply sloping glabellar tongue. The anterior area of the fixed cheek and preglabellar area are wider, and the outline of the anterior margin is bluntly pointed rather than rounded. The free cheek (Pl. 19, figs. 6, 10) may be distinguished most readily by the subangulate outline of the anterolateral margin, and by the sharp edge along this margin, formed by the acutely angulate junction between the sloping dorsal surface of the free cheek and the doublure. The posterior margin of the free cheek has a less prominent projection and makes a larger angle with the inner margin of the librigenal spine. The characteristic pit is present in the outer surface of the anterior part of the doublure. Successively smaller cranidia [sagittal length respectively 1.26 mm. (Pl. 19, fig. 8), 1.03 mm., (Pl. 19, figs. 5, 7)] differ principally from that described in the presence of the crescentic area of fixed cheek between the axial furrow and the palpebral furrow. Free cheeks associated with these cranidia are similar to those of larger size, and show the pit in the doublure. The smallest cranidium placed here (Pl. 19, figs. 1, 2), probably that of degree 0, is of length (sag.) 0.85 mm. It differs from cranidia of degree 0 of *R. caelatus* (Pl. 3, fig. 9) in that the anterior cephalic spines are longer and slimmer, not curved, and in that short, bluntly pointed fixigenal spines are present. A few examples of cranidia of the same size (Pl. 19, figs. 3, 4), lack the anterior cephalic spine, have the anterolateral margin smoothly curved, but are otherwise indistinguishable. Evidently the anterior cephalic spine is lost abruptly between moults.

Hypostome, thoracic segments and pygidium unknown.

Discussion. Inspection of the figures will show that the original of Plate 6, figures 20-22, of length (sag.) 2.13 mm., the smallest cranidium referred to *Robergiella sagittalis* n. gen., n. sp., might be considered to be a larger growth stage of the original of Plate 19, figure 9. The latter is the largest cranidium, length (sag.) 1.84 mm., placed in "remopleuridid gen. et sp. ind." Thus the series placed here might be the early developmental stages of *Robergiella sagittalis*. However, these two groups of specimens do not occur together at any one locality, though both come from the lower part of the Edinburg formation. Without more complete developmental series of both groups a decision as to whether or not they belong to two separate species cannot be made. Should they prove to be a single species, then the early development of the cephalon (remopleuridid gen. et sp. ind.) is more like that of *Remopleurides* than that of *Robergia* (Pl. 18, figs. 16, 17, 20, 21).

Distribution and Relationships of Remopleuridid Species from Virginia

Remopleurides appears first in the silicified material in the Upper Lincolnshire limestone, where it is represented by a single species, *R. asperulus*. In the Lower Edinburg limestone a great variety of remopleuridid species appear suddenly. There seems little doubt but that *Remopleurides caelatus* (the most abundant), *R. caphyroides,* and *R. eximius* are distinct species.

As noted above, the specimens included under *R. simulus* may be sexual dimorphs of *R. eximius* or they may be a further distinct species from Lower Edinburg limestone. *R. eximius* is so like the species from the Upper Lincolnshire that it is presumed to be its descendant. The antecedents of the other species are not known. In addition, in the Lower Edinburg limestone, *Robergia major* and *Robergiella sagittalis* are present. The abundance of types of remopleuridids in the Lower Edinburg limestone may be ascribed partly to their having come from a considerable variety of localities, but at all these localities the trilobite fauna is richer and more varied than at higher levels in the Edinburg or in the formations immediately below or above.

In the Oranda limestone, remopleuridids are not known, but in the succeeding lower part of the Martinsburg limestone one species, *Remopleurides plaesiourus*, is quite abundant. This species is exceedingly similar to *R. caelatus* and is most probably descended from it.

Comparison of the Virginia Remopleuridid Species with Those of other Areas

The morphological characters displayed by the Virginia species are seen in slightly different combinations in species from northwestern Europe across into China (Lu, 1957, pl. 153, figs. 14, 15, 16). Raymond (1925, p. 57) referred some material from Virginia to a Canadian species, and also erected the species *R. rugicostatus* on material from the Wilderness stage (Cooper, 1956) of Tennessee. This species is extremely like the slightly older *R. simulus* n.sp. (see above).

The type species of *Remopleurides*, *R. colbii*, from the Middle Ordovician of Eire (Whittington, 1950b, pp. 540-543, pl. 70, figs. 1, 2, 4, 5), has a cephalon (including hypostome) quite like those of the present *R. caphyroides*. However, the thorax and pygidium of *R. colbii* recall those of *R. eximius* (Pl. 14) and *R. simulus* (Pl. 17). There is a remarkable similarity between one specimen that I referred doubtfully to *R. colbii* (Whittington 1950b, pl. 69, figs. 5, 6), and the holotype of *R. eximius*. A second species from the same horizon in Eire is *R. dorsospinifer* (Whittington, 1950b, pl. 69, figs. 7-10), a species that has much in common with *R. caelatus* (Pls. 1, 2) and *R. plaesiourus* (Pl. 5, figs. 1-15). In 1950 (p. 542) I held the view that *R. dorsospinifer* might belong to a genus separate from *Remopleurides*. I would now expand the limits of *Remopleurides* and include *R. dorsospinifer* within this genus. A third species from Eire, *R. longicostatus* (Whittington, 1950b, pl. 70, figs. 3, 6), has the long genal spines (Pl. 7, fig. 4) and the long bladelike pleurae (Pl. 9, figs. 1-5, 7, 8) characteristic of *R. caphyroides*.

From Middle Ordovician horizons in Scotland come *Remopleurides girvanensis* Reed, (1903, pp. 39-41, pl. 6, figs. 8-15) and

R. biaculeatus Tripp (1954, pp. 664-666, pl. 2, figs. 1-12). The former of these species is like *R. eximius* from Virginia. *R. biaculeatus* bears a strong resemblance to *R. caelatus*, and Tripp's description includes such details as the pit in the cephalic doublure and the median boss and oval areas of the hypostome. Thorslund (1940, pl. 7) illustrated remopleuridids from the Middle Ordovician of Sweden. The cephalon of *R. validus* Thorslund is like that of *R. caelatus*, whereas the pygidium of this species is more like that of *R. eximius;* the pygidium of *R.* cf. *latus* Olin is more like that of *R. caelatus*. The thorax of *R. nanus elongatus* (Öpik, 1926, pl. 2, fig. 17), from the Middle Ordovician of Estonia, is like that of *R. simulus*, the pygidium (Öpik, 1937, pl. 24, figs. 1, 2) of *R. caelatus* type. There is evidently a closely related group of species of *Remopleurides* in the areas mentioned.

Quite similar species of *Robergia* are known in Oklahoma and the Appalachians (Cooper, 1953, pp. 22-24), Scotland and Sweden (Whittington, 1950b, pp. 543-4), in Middle Ordovician rocks, but do not seem to be known in Asia (I regard the illustrations referred to by Kobayashi, 1951, p. 20, as being of *Remopleurides*).

Superfamily TRINUCLEOIDAE Hawle and Corda, 1847

Trinucleidae and Raphiophoridae exhibit characters in common in both developmental and holaspid stages. In holaspides the occipital ring is narrow and lacks the doublure; in front of it the glabella expands forward and has the frontal part the most strongly convex. There are three pairs of subcircular or suboval muscle areas; the basal area is in many genera strongly impressed in the external surface, these impressions defining a narrow "neck" or a swollen ring, the occiput, in front of the occipital furrow; median pair is situated well up on the slope of the glabella, anterior pair small. Deep anterior pit. Cheek convex, posterior border defined by furrow which deepens distally and may form a pit; librigenal spine long; eye lobe bearing a compound eye absent, eye tubercle in some trinucleids; suture not passing across eye lobe but marginal or submarginal, free cheeks narrow (tr.) on dorsal surface, continuous ventrally, no median or connective suture. Hypostome subtrapezoidal in outline, convex middle body, narrow border defined anterolaterally and continuous around lateral and posterior sides; small wings. Seemingly hypostome not joined to cephalic doublure along a suture, but probably held closely beneath glabella by muscles.

Five or six thoracic segments, articulating furrow with a deep appendiferal pit, the horizontal pleurae bent down only at the extreme outer part, the doublure merely a curled-under edge, the pleural furrow strong. Articulating half ring lacking on first segment, which is bevelled anterolaterally. Pygidium subtriangular in outline with a gently convex, tapering axis reaching back to the rim. The larger part of the pleural regions is horizontal, the outer part bent down to form a steeply sloping border, the margin of this border typically sinuous, with a median posterior notch; doublure formed of the curled-under edge. Some ten segmental divisions may be revealed in the axis by up to five ring furrows and appendifers; muscle areas (commonly an inner and outer pair) may indicate further segments posteriorly; one to five pleural furrows. Apparently when enrolled, border of pygidium lay against inner edge of cephalic doublure.

The protaspides, described here for the first time, are similar in outline, convexity, and breadth of the gently convex axis. Up to three pairs of border spines may be present; in the cephalic portion the suture runs around the outermost edge of the pleural regions and narrow preglabellar area, posteriorly crossing the doublure in a sharp curve. In larger protaspides the glabella has the clavate form, the axis of the protopygidium is bulbous and vaguely defined, the pleural regions slope vertically posteriorly and have the median notch. Earliest meraspid cranidia display the clavate glabella with flat, steeply sloping sides and a median longitudinal keel, the occipital ring ill-defined. Convex cheek without border spines, posterior border best defined distally, by the pit. Suture is marginal and laterally has a slightly inwardly concave course. Alae, which are not evident in the protaspis, are relatively large and gently convex in trinucleids, *Ampyx, Ampyxina,* and *Raymondella,* but not in *Lonchodomas.* Small transitory pygidia have a transverse outline, a bulbous, ill-defined axis that does not taper posteriorly, the pleural regions slightly bent down beside the posterior part of this axis, the outermost parts of the pleural regions bent down to form the border. Typically there is a median posterior notch in the outline.

Between the protaspis and degree 0, border spines are lost while at degree 0 the frontal glabellar spine of raphiophorids makes its appearance. In immediately succeeding degrees the trinucleid fringe develops rapidly. Thus some familial (e.g. the raphiophorid frontal glabellar spine) and generic (e.g. the glabellar carina of *Lonchodomas*) characters are evident at degrees 0 to 1, whereas other generic characters (e.g. the expansion of the frontal part of the glabella in *Tretaspis* and *Raymondella,* or the fringe of *Tretaspis*) develop in immediately succeeding degrees.

Family TRINUCLEIDAE Hawle and Corda, 1847

The common characters of holaspides of this family have recently been discussed (Whittington, 1959, p. O420). The present material, however, shows the development more completely and, by virtue of the excellent preservation, in greater detail than heretofore. The protaspides of *Cryptolithus* (Pl. 23, figs. 11-16) and *Tretaspis* (Pl. 26, figs. 2, 3, 5, 6, 8-13) show a considerable likeness in form. Only degree 0 specimens were previously known, and they have no marginal spines on cheek lobe or transitory pygidium. The presence of such spines in the protaspis is thus unexpected, and their loss at the end of the protaspid period abrupt. The development of the glabella is similar in each genus — in the protaspis it has only a slight anterior expansion, this expanson increasing and a strongly convex, sharply carinate, form appearing early in the meraspid period in *Cryptolithus* (Pl. 23, figs. 1, 2, 9), in the late protaspid period in *Tretaspis* (Pl. 26, figs. 10, 13). Only in holaspides does this carinate form give place to a convexity that is rounded in transverse profile, while the anterior expansion becomes fully developed. Alae are not discernible in the protaspis, are largest at degree 0 (Pl. 23, fig. 6; Pl. 27, fig. 1), and are progressively reduced so that little or no trace of them remains in the largest holaspides (Pl. 20, figs. 4, 6; Pl. 24, fig. 1).

The border of the cephalon is at first a rolled margin, traversed on the upper surface by the marginal suture and at the genal angle continuous with the genal spine. A concentric row or rows of pits first appear (in late degree 0 and degree 1; Pl. 23, figs. 5, 7; Pl. 27, figs. 13, 19) in a deep trough which is immediately adjacent to the cheek lobes and preglabellar area, and there is a corresponding trough in the lower lamella. The first complete concentric row or rows has almost the same number of pits as in the holaspis. The fringe widens rapidly as additional concentric rows are added, and not until three such rows are present is the girder apparent (Pl. 22, figs. 1, 2, 5, 6, 10, 12; Pl. 28, figs. 1-4). The complete number of concentric rows appears fairly early in the meraspid development, and in the later meraspid and early holaspid periods relatively few pits are added and the fringe assumes its characteristic holaspid form — for example (compare Pl. 22, figs. 1, 2, with Pl. 20, figs. 4, 6, 7; Pl. 28, figs. 1-8 with Pl. 24, figs. 1-5), the lower lamella becomes sharply flexed at the girder as the latter becomes deeper, cheek roll and brim appear in *Tretaspis,* and concentric ridges and radial ridges and sulci appear in the upper and lower lamellae. The abrupt appearance of a new, complete concentric row of pits in the early meraspid degrees is accompanied by a marked increase in dimensions. Thus the early meraspides of *Cryptolithus* show a series of size groups corresponding to those with one, two and three complete concentric rows. It is hoped that the abundant material of *Cryptolithus* will permit a more detailed study of this phenomenon.

Early transitory pygidia (Pl. 23, figs. 3, 8, 10; Pl. 27, figs. 14, 15, 17, 18, 21, 23) have a bulbous axis which is broad and rounded posteriorly, the posterolateral parts of the pleural regions are bent down steeply, and the shallow median posterior notch gives a bilobate outline. During the meraspid period (Pl. 23, figs. 17-19, 21, 23; Pl. 27, figs. 20, 22, 24, 25) the outline becomes triangular, the axis gradually assumes the tapering form, the rings are better defined, the pleural regions become horizontal, with the outer parts bent down in the characteristic vertical border; in posterior view the outer margin of this border is sinuous and has a median notch.

While these parallels can be drawn between the development of *Tretaspis* and *Cryptolithus,* it is nevertheless evident that from the protaspis onwards the two genera can readily be distinguished. In the early meraspid degrees, for example, *Tretaspis* already exhibits such features as the relatively wider and more convex frontal part of the glabella, the more prominent eye tubercles and eye ridges, and the wider lateral part of the fringe with more pits.

Subfamily CRYPTOLITHINAE Angelin, 1854

Genus CRYPTOLITHUS Green, 1832

CRYPTOLITHUS TESSELATUS Green, 1832

Plates 20-23

Cryptolithus tesselatus, Whittington, 1941a, pp. 29-30, pl. 5, figs. 2, 15, 17, 18; Whittington 1941b, pp. 509-511, pl. 75, figs. 1-26, 46.

Material. Martinsburg shale, localities 9-12; all figured material in U. S. National Museum.

Description. All the features mentioned in my previous descriptions may be seen in the present illustrations. The radial plates between the pits of E_1 and the concentric ridge between I_1 and I_2 are both generally present (Pl. 20, figs. 2, 3, 4), though one or other may be poorly developed and in occasional specimens neither is prominent (Pl. 20, fig. 6). On the external surface of the glabella (Pl. 20, fig. 6), the network of raised ridges is strongly developed in the median and anterior areas: it is absent from the lateral slopes (compare for example *Reedolithus quebecensis* Stäuble, 1953, figs. 4, 5). On the internal surface (Pl. 20, figs. 9, 11; Pl. 22, fig. 7) there are small appendifers present in the occipital furrow and adjacent to the posterolateral margin of the occiput. In addition three pairs of muscle areas may be observed on the externally smooth, sloping, lateral parts of the glabella (Pl. 20, fig. 6), each suboval in outline, the basal pair situated in the lateral portions of the occiput, the median area a short distance in front, subcircular in outline, the anterior area smaller, situated at about the midlength of the glabella. These muscle areas may be distinguished on a few specimens by their slightly different color (Pl. 20, figs. 9, 11), and are not depressed as are the corresponding areas in *R. quebecensis* (Stäuble, 1953, figs. 4, 5). The median glabellar tubercle (Pl. 20, fig. 10) is a low, raised mound in the center of the network on the external surface of the glabella. Pits like those seen in the corresponding tubercle in *Tretaspis* *seticornis* (Størmer, 1930, pp. 85-87, fig. 37) have not been seen. External surface of cheek lobe usually smooth (Pl. 20, fig. 4), but an occasional specimen has shallow pits irregularly and closely scattered (Pl. 20, fig. 6). On neither the external nor the internal surface of glabella or cheek lobes have the raised lines described by Ruedemann (1916, pl. 35, figs. 6, 7) been observed.

The pits in each lamella of the fringe are opposing, deep, their flat bases in contact (Pl. 20, fig. 8; Pl. 21, fig. 17); during moulting the marginal suture separated the flat bases of opposing pits. Well preserved specimens show a minute hole in the center of the flat base of the pit, and in specimens in which both lamellae of the fringe are present this tiny opening can be seen connecting opposing pits. This opening appears to be an original structure and not the result of abrasion. The pits in harpids seem to have the same structure (Evitt, 1951, p. 607).

Three small specimens of the hypostome have been recovered (Pl. 21, figs. 18, 19), one of them approximately in position in a cephalon (Pl. 21, fig. 16) which is smaller than that of a degree 3 example (Pl. 21, figs. 14, 15). The hypostome was not found during the previous investigation (Whittington, 1941b, p. 517) and it is rare in the present material. Outline subsquare, slightly narrower across anterior margin than across posterior. Anterior margin curved convexly forward, forming a continuous curve with the slightly inwardly-directed lateral margin, there being no projecting anterior wing; posterior margin curved convexly backward. Middle body moderately convex, steeply sloping laterally; no anterior border, lateral border becomes defined by a shallow furrow anterolaterally and widens backward, merging with the broad posterior border which is narrowest in the midline; posterior border furrow shallow medially, becoming broad and deeper distally. Edges of lateral and posterior borders bent upward vertically, no doublure. In the specimen in which it is in place, the size and forwardly converging lateral margins enable the hypostome to rest a short distance inside the glabellar cavity; this position may approximate the position in life. There is no suggestion that the hypostome fitted against the inner margin of the lower lamella of the fringe along a hypostomal suture; indeed, if the posterior border of the pygidium came into contact with the inner edge of the lower lamella during enrollment, such a fit is not possible (Whittington, 1941b, p. 517).

Articulating half ring not developed on the anterior thoracic segment (Pl. 20, fig. 5; Pl. 21, figs. 1-3), present on succeeding segments (Pl. 21, figs. 4-7); deep appendiferal pits and stout appendifers, articulating devices in the axial furrow; facet exceptionally large on the anterior segment where it fits beneath the posterior border of the cephalon (Pl. 20, figs. 5, 7; Pl. 21, fig. 8), smaller on succeeding segments (Pl. 21, fig. 7); a posterior excavation in the narrow doublure receives the facet during enrollment. The articulating furrow of the pygidium (Pl. 21, figs. 9-13) also bears deep appendiferal pits and stout appendifers; on the first ring furrow the appendifers are faint; on the third they are replaced by an elongate-oval muscle scar; the succeeding ten or so rings are indicated by two pairs of muscle areas—an inner, smaller pair and a larger, outer pair which appear as shallow elongate depressions on the external surface.

Development

Protaspis. The originals of Plate 23, figures 11-16, and a number of additional specimens from localities 10 and 12, are believed to be the protaspis of *Cryptolithus tesselatus.* The other species occurring at these localities have been listed above, and the protaspides of *Diacanthaspis cooperi* (Whittington, 1956, p. 214) and *Flexicalymene senaria* (Whittington, 1941b, p. 495) have been described. From our unpublished studies of the ontogenies of the remaining species, or of species closely related to them, W. R. Evitt and I conclude that, by elimination, this protaspis can only be that of *C. tesselatus.*

Exoskeleton strongly convex, laterally and posteriorly sloping vertically or even slightly overhanging the margin. Widest at about one-third the length, posterior portion tapering more than the anterior, anterior margin with a median concavity in the outline. Glabella clearly outlined by shallow axial, preglabellar and post-occipital furrows, expanding slightly forward, gently convex, most strongly so at about the midlength (which point is in front of widest part of protaspis and seems to be surmounted by the median tubercle, Pl. 23, fig. 13), rounded anteriorly, separated only by the preglabellar furrow from the anterior sutural margin. Anteromedian part of protopygidium convex, steep slope down to post-occipital furrow, anterolaterally a line of change of slope runs out and back from the posterolateral angle of the glabella (Pl. 23, fig. 12); posterolaterally this median convexity dies out. Steep posterolateral slopes of protopygidium continued by narrow, curled doublure (Pl. 23, fig. 16); this doublure extends forward a short distance and is then cut off by a suture which crosses it in a curve convex backward; suture continues forward to bound lateral and anterior margins of shield. Free cheeks and hypostome unknown. Close to the posterior margin of the protopygidium, in the midline, a pair of thornlike spines (Pl. 23, figs. 12-14), their bases close together; each spine is directed backward and slightly inward, one directed horizontally and the other upward so that distally they cross. On the ventrally-facing doublure immediately below the bases of these spines there is a pair of ventrally-directed small tubercles (Pl. 23, figs. 14, 16). Posterolateral margins scalloped in outline, with a median posterior concavity. External surface finely granulate. Tiny crystals of quartz are scattered over the surface of the specimens, and in some cases give the appearance of a row of border spines. Examination of several specimens, however, shows that the position in which they occur is not consistent and that they are truly scattered grains.

Degree 0. Next largest are enrolled exoskeletons, lacking the lower lamella of the fringe, which are of degree 0 (Pl. 23, figs. 6, 8-10; maximum width across cheek lobes, 0.98 mm., which is considerably greater than maximum width of protaspis, 0.51 mm. in original of Pl. 23, figs. 14, 16). Cranidium subsemicircular in outline, more than twice as wide (tr.) as long; convex anterolateral part of cheek lobe sloping steeply. Glabella much more strongly convex than in the protaspis, with a rounded longitudinal crest and flattened, steeply sloping sides; occipital ring narrow (sag. and exs.), curved convexly backward, occipital furrow shallow medially, distally running into a deep pit; relatively large median glabellar tubercle situated on the highest point slightly behind the midlength. Ala of length (exs.) slightly greater than half that of the glabella, gently convex, subtriangular in outline, situated between the shallow axial and alar furrows, not separated by a furrow from the posterior border and distal part of the occipital ring.

Relatively large lateral eye tubercle, combined with a broad eye ridge, running inward and forward to axial furrow. Posterior border and posterior border furrow well defined, posterior border with characteristic backward curvature distally just inside where it is crossed by the suture. Marginal suture curves around genal angle and bounds narrow, outermost part of cheek lobe, which is gently sloping; in front of preglabellar furrow is a slight inward concavity in the course of the suture corresponding to that seen in the protaspis.

Pygidium with axis not tapering, posterior portion the most convex and bluntly rounded, axis merging, in slope which is concave upwards, with pleural regions, latter horizontal laterally. First axial ring outlined by ring furrow. Two pairs of pleural furrows extend a short distance out from axial furrows; narrow raised border to pleural regions, the outline of the steeply-sloping margin displaying a shallow median notch. External surface granulate, row of tiny granules around upper surface of pygidial border.

Larger meraspides. Cranidia having a width (tr.) between about 1.4 mm. and 3.0 mm. fall into three size groups, the successive groups having one (Pl. 23, figs. 1-5, 7), two (Pl. 22, figs. 10-12), or three (Pl. 22, figs. 1-4) concentric rows of pits respectively. These size groups do not necessarily correspond to degrees. There are individuals having one row of pits which belong to degree 1 (Pl. 23, figs. 1-4), but the smallest specimen described previously (Whittington, 1941b, p. 510, pl. 75, fig. 5) had one row of pits but belonged to degree 0. Similarly some specimens having three concentric rows belong to degree 3 (Pl. 21, figs. 14, 15) while others belong to degree 2 (Whittington, 1941b, pp. 510-11, pl. 75, fig. 4).

In the cephala with one row of pits the glabella has begun to assume the characteristic clavate form, is more strongly keeled, with flat steeply-sloping sides, and retains the large median glabellar tubercle. The ala is well developed, outlined distally by a curving alar furrow which has a steep slope on the outer side. Convex cheek lobe having the coarse reticulate raised lines on the external surface, the network coarsest on the inner part of the lobe. The gently sloping outermost part of the cheek lobes and frontal area of the cranidium is relatively wider, and the single row of pits is close to the inner edge.

Cephala show that the marginal band and lower lamella form a continuous rolled structure with this outer part of the cranidium, the suture running along the upper, outer margin of this roll. On the lower lamella the single row of pits lies at the bottom of the deep concentric groove, the inner part of the lamella being flexed to slope outward and downward; the margin curled; outline of this margin exhibiting a median projection which corresponds in shape with the notch in the posterior outline of the transitory pygidium (compare Pl. 23, fig. 7 with Pl. 23, fig. 3). At the genal angle the tubular structure of the fringe is continued by the genal spine, which is curved and directed backward.

The cephala with two rows of pits (Pl. 22, figs. 10-12) show little morphological change except that the ala is relatively smaller. The upper lamella of the fringe slopes outward and downward at a more gentle angle than the outer part of the cheek lobe, the marginal band is traversed by parallel raised lines, and the two rows of pits in the lower lamella are situated in a deep but broader groove. Inside innermost row of pits edge of lower lamella is tightly rolled to form a thickened, projecting edge.

In cephala with three rows of pits (Pl. 22, figs. 1-4), the median glabellar tubercle is relatively smaller and the median occipital spine has appeared for the first time as a large tubercle; the lateral eye tubercle and eye ridge are somewhat less prominent, and the ala is much reduced in size but proximally still merges into the distal part of the occipital ring and innermost part of the posterior border. The coarse reticulate pattern of the external surface is now clearly visible on the median part of the glabella, as well as the cheek lobe, and on the latter the reticulation extends down into the alar and axial furrows on each side of the ala; the reticulation is coarsest on the inner part of the cheek lobe, on the outer part it becomes finer, and there is a smooth band on the extreme outer slope. On the lower lamella (Pl. 22, fig. 2) the rows of pits are no longer at the base of a deep groove; the outer row E_1 is separated from the inner rows by the low but distinct girder, which at the genal angle runs out for a short distance along the under side of the genal spine. The inner edge of the lower lamella is tightly curled, the outline no longer having the slight median backward projection, but transverse or with a faint median notch. The single cephalon with the hypostome in position (Pl. 21, fig. 16) has three concentric rows of pits and belongs to this group in the size series.

Development of the transitory pygidium (Pl. 23, figs. 17-19, 21) is best shown by the isolated specimens. Four or five axial rings are defined by deep narrow axial furrows. Appendifers are present on the articulating furrow and on the first one or two ring furrows. Axis changes gradually in shape, becoming backwardly tapering and losing the strong convexity of the posterior part. At no time are distinct axial furrows developed. The inner part of the pleural region is horizontally extended, the outer part narrow and bent steeply down; at the flexure is the rim and a broad shallow groove inside this rim. Up to five pairs of deep, narrow, pleural furrows may be observed, in the smaller specimens the outline having a slight forward concavity. As size increases, these pleural furrows extend farther out, ultimately reaching the marginal furrow. Inter-pleural grooves are extremely faint, indicated only by a short depression situated just inside the marginal furrow, and best visible in the larger specimens. A row of small tubercles along the upper surface of the rim, and the steep outer parts traversed by raised lines. The slight median concavity seen in the posterior outline of the pleural regions in dorsal view is soon lost; at the same time the shallow median posterior notch in the margin of the steeply sloping outer parts becomes evident and increases in depth as size increases.

Larger meraspides and holaspides. Beyond the size group at which three concentric rows of pits first appear, changes that take place in the cephalon (Pl. 20, figs. 2-4, 6, 9, 11; Pl. 22, figs. 5-9) are relatively minor. The glabella gradually assumes the holaspid form, the occiput and muscle areas become visible, the median glabellar tubercle becomes relatively smaller while the median occipital spine lengthens. Both the ala, eye tubercle, and eye ridge gradually disappear. The raised network on the cheek lobe, which is coarsest and most prominent on the inner part, extends into the axial furrow, but as size increases it gradually disappears and in the largest specimens either the cheek lobe is smooth or it bears scattered shallow pits (Pl. 20, fig. 6).

Pits are added to the fringe only along the inner lateral and posterolateral areas. On the upper lamella the concentric ridge between I_1 and I_2 appears first, and later the raised radial ridges between the pits of E_1 become evident. On the outer surface of the lower lamella the girder becomes much stouter, especially anteriorly, projecting as a prominent ridge about which the lower lamella is flexed so that the inner part slopes upward and inward steeply. The ridges which separate I_1 from I_2, and I_2 from I_3, in the anterolateral and lateral part of the lower lamella also develop gradually. The inner edge of the lower lamella continues to be tightly rolled, but in ventral aspect the outline bears a decided shallow notch medially. This notch develops at the same time as the median posterior region of the pygidium begins to develop a slight projection (compare Pl. 22, fig. 5 with Pl. 23, fig. 20). During enrollment the steep outer parts of the pleural regions of the pygidium lie against the tightly curled inner edge of the lower lamella; study of the illustrations will show that the changes in outline of these two parts of the exoskeleton complement each other.

On small holaspid pygidia (Pl. 23, figs. 20, 22, 23) some eight axial rings are outlined by axial furrows which become shallower posteriorly; up to four pairs of narrow, deep, pleural furrows may also be observed. The largest pygidia (Pl. 21, figs. 10-13) are relatively longer than this small one, the pleural regions show the first and only a faint second pleural furrow, and the border retains the characteristic sinuous outline.

Measurements of the abundant specimens of the small developmental stages, and counts of the pits and their distribution, form a separate study which will be published elsewhere (cf. Whittington and Hunt, 1958, abstract).

Subfamily TRETASPIDINAE Whittington, 1941

Genus Tretaspis M'Coy, 1849

Tretaspis sagenosus n. sp.

Plates 24-27; Plate 28, figures 1-8.

Tretaspis reticulatus, Whittington, 1941a (part), pl. 6, figs. 30, 34, 35.
Ampyxina elegans Cooper, 1953 (part), pl. 4, figs. 13, 17.
Holotype. USNM 137690 (Pl. 24, figs. 1-5), locality 16.

Other Material. Paratypes USNM 137691a-c; all figured material in U. S. National Museum.

Geological Horizon and Localities. Lower Edinburg limestone. Localities 2, 3, 4, 7, 14a and 16; road to Cherry Grove, 4 miles northwest of Linville, Rockingham Co., Va.

Description. Cephalon (Pl. 24, figs. 1-5) subsemicircular in outline, short genal prolongations and backwardly directed genal spine; length (sag.) and maximum height about half maximum width. Glabella expanding forward from the occipital ring to a width (at about one-third the length) almost twice as great, portion in front of occiput subhemispherical. Occipital ring narrow (sag.), backwardly curved, sloping gently forward to occipital furrow; latter shallow medially, distally deepening into a pit; occiput slightly narrower (tr.) than occipital ring, of about same length (sag.), gentle independent convexity; basal lateral glabellar furrow commencing a short distance inside the axial furrow, directed inward and forward, short and deep; second lateral glabellar furrow situated a slightly greater distance inside the axial furrow, and in the form of a deep subcircular pit; median glabellar lobe between lateral furrows strongly convex and merging anteriorly with the convex frontal lobe; third lateral glabellar furrow a small pit also situated a short distance inside the axial furrow and low on the steeply sloping flank of the frontal lobe; maximum width of glabella in front of third glabellar furrows.

Axial furrow shallow, broad posteriorly, a slight swelling adjacent to the extremity of the occipital ring probably represents the ala; shallow anterior pit. Inner part of cheek lobe gently convex, outer part sloping extremely steeply anterolaterally; posterior border furrow broad, deep, transversely directed, posterior border narrow, convex, flexed downward distally before it joins the internal rim of the fringe.

Fringe includes steeply sloping cheek roll and much less steeply sloping brim, entire fringe arched up medially; upper lamella with gently convex cheek roll and gently concave brim, narrow upper external rim; broad marginal band joins this rim to lower external rim, lower lamella subdivided by prominent girder which is deepest anteriorly where the cheek roll and brim lie at an acute angle to each other; posterolaterally the angle becomes oblique where the girder is less strong; along internal margin of lower lamella a narrow convex rim which is highest anteriorly and anterolaterally; between this rim and the girder the cheek roll is deeply concave anteriorly, but posterolaterally it becomes flat; brim between girder and lower external rim flat; external and internal rims meet at tip of prolongation and are continued by a long slim genal spine which is subtriangular in section, the three angles of the spine being continuous respectively with the external rim, the internal rim, and the girder. Marginal suture traverses upper edge of marginal band, at tip of prolongation curving to run along upper surface of internal rim, crossing this rim to reach the posterior margin of the cephalon about in line (exs.) with the distal part of the cheek lobe.

Fringe with two external rows of pits (E_1 and E_2); in the holotype each row has twenty-six pits on the right side, the twenty-sixth pit being a large one at the posterolateral extremity that is common to the two rows. Anteriorly and anterolaterally four rows of pits internal to the girder (I_1 to I_4), these pits being radially arranged with those of E_1 and E_2; the radial arrangement is undisturbed as far as R_{16} on each side, and narrow concentric ridges on the upper lamella separate the pits in each row, the ridge between I_3 and I_4 dying out at about R_{12} to R_{15}, the outer two ridges continuing to about R_{18} where they merge with a network of raised ridges surrounding the pits in the posterolateral region. In this latter region, beyond R_{16}, intercalation of pits makes the arrangement irregular so that the separate internal rows cannot be distinguished. On each side of the holotype at about R_{16} the row I_5 can be recognized because I_1 bifurcates. About nine pits along the posterior margin of the fringe. On the upper lamella the pits of E_2, E_1, and I_1, as far out as R_{16}, are in deep radial sulci; outside R_{16} only E_1 and E_2 are in radial sulci and a low concentric ridge separates E_1 from I_1. On the cheek roll of the lower lamella in the anterior and anterolateral regions the pits are in deep radial sulci.

External surface of glabella and cheek lobe (Pl. 24, fig. 7; Pl. 25, fig. 2; Pl. 26, fig. 1) bearing a network of strongly raised lines, network coarsest on the crest of the glabella and the inner part of the cheek lobe, becoming finer on the flanks of the glabella and not extending into the lateral glabellar furrows, absent from the axial and posterior border furrows, becoming finer distally on the cheek lobe and absent from the outer part. Small median glabellar tubercle situated at about half the length; behind this tubercle the raised lines form an almost straight median line that extends back to the occiput (Pl. 25, fig. 2). Eye tubercle situated opposite the median lateral glabellar furrow and far out on the cheek lobe on the edge of the steep anterolateral slope. Raised lines of the network forming a zig-zag ridge (the eye ridge) that runs inward and forward in the direction of the anterior lateral glabellar furrow.

Internal surface of glabella and cheek lobes (Pl. 24, fig. 2; Pl. 26, fig. 4) showing faint impression of network, deep pit at extremity of occipital furrow, and posterior and median lateral glabellar furrows form raised platforms; anterior glabellar furrow barely visible, anterior pit forming a small boss. No doublure on occipital ring or along posterior border. Fine subparallel raised lines traverse the girder and the ridge at the inner margin of the lower lamella (Pl. 25, fig. 4), and these fine lines continue along the angles of the genal spine.

In some specimens the muscle areas are distinguishable by their slightly darker color (Pl. 25, fig. 1). The seemingly smooth axial and posterior border furrows are in some specimens (Pl. 26, fig. 1) finely granulate, and similar fine granules run along the crests of the network of ridges (Pl. 25, fig. 2) as well as in the occipital furrow and along the posterior border. External surface of lateral eye tubercle apparently smooth; in the median tubercle of the glabella a suggestion (Pl. 25, fig. 2) of one or two tiny depressions, perhaps similar to those described in *Tretaspis seticornis* by Størmer (1930, p. 87, fig. 37). The structure of the pits in the fringe (Pl. 25, figs. 3, 4) is similar to that described in *Cryptolithus*, that is, the base of the pit is flat and may be pierced by a tiny median opening.

Three or four isolated thoracic segments (Pl. 24, figs. 6, 8, 9, 11, 12, 14, 15) have been recognized, both because of the similarity in form of the axial ring and articulating furrow to the occipital ring and furrow of the cephalon, and because of the small pygidium from locality 2 which is articulated with two segments (Pl. 24, figs. 10, 13). Axial ring narrow (sag. and exs.), moderately convex, articulating furrow deep and broad, descending distally into a deep appendiferal pit which projects ventrally as a triangular appendifer, slightly thickened at the tip. Articulating half ring short (sag.), that of the first thoracic segment narrower (tr.) than the axial ring. Pleura extends out horizontally, distally bent down in two stages, the first gently sloping, the outermost portion vertical, the margin curled under to form an extremely narrow doublure. Pleural furrow broad and deep, running out transversely to the extremity of the pleura, flanked by ridges the anterior of which is the wider (exs.); narrow posterior flange which extends out from the axial furrow to about two-thirds the width of the pleura. Anterolateral part of first thoracic pleura cut off diagonally and faceted so that it fits beneath the bent-down extremity of the posterior cephalic border; smaller facets on succeeding segments, a small depression in the posterior part of the doublure receives these facets during enrollment.

Pygidium (Pl. 24, figs. 16-19) about three times as wide as long, anterior margin transverse, posterolateral margins evenly rounded; axis gently convex, extending back so that tip merges into narrow rim, border bent down steeply. Five axial rings outlined by six ring furrows (counting the articulating furrow as the first) which are shallow medially and distally descend into a deep appendiferal pit, this pit situated a short distance inside the axial furrow. A seventh ring furrow is outlined by two pairs of subcircular darker areas, the inner pair being closer to the midline and smaller; on the external surface of some specimens these two pairs of dark spots are combined in one pair of elongate depressions. In one specimen (Pl. 25, figs. 5, 6) ring furrows 8 to 11 are indicated by darker muscle areas, the eighth by a median elongate dark area, the ninth by a similar median area and an outer pair of spots, the tenth and eleventh by two distinct pairs of dark spots. The dark areas indicating the ninth ring furrow are on the rim at the tip of the axis, those marking the tenth and eleventh on the upper part of the border.

Four pairs of pleural furrows are present, the first running outward and slightly backward, distally curving back and becoming shallower, not reaching the rim. The next three furrows are successively shallower, directed slightly more strongly backwardly, and display the slight distal curvature. In posterior view border of the pleural regions has a sinuous margin with a shallow median notch. On the inner surface (Pl. 24, fig. 16) appendifers are strongly developed on the articulating furrow, and are successively smaller on the three succeeding ring furrows. External surface of thorax and pygidium apparently smooth, except for the fine raised lines that run along the outer parts of the pleural regions.

Discussion. The above description is based on the largest specimens in the present material, which include cephala, thoracic segments and pygidia from locality 16, the largest cephalon being of maximum width about 1 cm. The originals of Cooper's (1953, pl. 4) figures 13 and 17, from locality 7, are like the original of Plate 24, figure 10, and unlike the pygidium here attributed to *Raymondella elegans* (Pl. 36, fig. 33), and so are attributed to *Tretaspis sagenosus* n. sp.

The description of the number and arrangement of the pits in the fringe is based on the holotype cephalon. Earlier (Whittington, 1941a, p. 29, pl. 6, figs. 30, 32, 34, 35) I referred material from similar horizons in Virginia to *Tretaspis reticulatus* Ruedemann, 1901. This latter species, from the Rysedorph conglomerate of New York State, has been redescribed by Stäuble (1953, pp. 210-211, figs. 21-24). The incomplete cephala on which *T. reticulatus* is based are of about the same size as the holotype cephalon of *T. sagenosus* (Pl. 24, figs. 1-5), and appear extremely similar. They may be distinguished, however, by the occurrence in *T. reticulatus* of I_5 as a complete row and I_6 laterally. The single incomplete cephalon from the lower "Athens" near Tenth Legion, Virginia (USNM 97436; Butts, 1941, p. 75, pl. 82, fig. 8; Whittington, 1941a, pl. 6, fig. 32), is of maximum width about 1.75 mm., and is exceedingly like *T. reticulatus* in having I_5 complete and I_6 present laterally. The silicified specimens described in 1941 (Whittington, 1941a, pl. 6, figs. 30, 34, 35), from the lower Edinburg limestone, four miles northwest of Linville Station, Va., display only I_4 as the innermost complete row, and in this respect are similar to many of the specimens in the present collection. Accordingly, these silicified specimens have been distinguished as a separate species, but the number of relatively large cephala with the fringe complete on at least one side is few, and inadequate to establish the amount of variation in the number and arrangement of the rows of pits. One or two examples will suffice to show that considerable variation does occur:—

a) Cranidium, maximum width 1 cm. (Pl. 24, fig. 7; Pl. 26, fig. 4), is like the holotype in having 25 or 26 pits in the complete rows on each side, I_5 commencing at about R_{16}. A single pit is intercalated between the two pits of E_1 and E_2, between R_{18} and R_{19}; and in addition, between R_{10} to R_{20} on each side, a third external row, E_3, is developed by subdivision of the pits in E_2. The presence of E_3 in the new species is a unique feature within the genus.

b) Incomplete cranidium, width of about 7 mm. (Pl. 26, fig. 1), displays some peculiarities, for in R_5 and R_7 there is no pit in E_2, only a pit in E_1; in R_8 and R_9 two pits are missing in I_4. However, in R_4 to R_7 (adjacent to the axial furrow) a few pits of I_5 appear.

c) Cephalon, maximum width 4.8 mm. (Pl. 26, figs. 14-16), from locality 2, has between 27 and 28 pits on each side in the external rows; E_3 is present between R_8 and R_{25} on the left side and between R_2 and R_{25} on the right side. This specimen displays by far the best development of E_3. I_5 commences at R_{16}, but is recognizable because I_1 divides into two rows beyond this radius, rather than because I_4 divides.

d) Fringe of left side (Pl. 26 fig. 7), from locality 2. This is much like the holotype and other specimens from locality 16 and has 26 pits on each side in E_1 and E_2. I_5 appears at R_{17}, again not because of the division of I_4 but because I_2 divides.

e) Part of cephalon displaying fringe on right side, from locality 14a (not figured) has 30 pits in E_1 and E_2, I_1 divides at R_{15}, and the row I_5 is complete. This latter feature at once recalls *T. reticulatus* and the present cephalon is of about the same size as Ruedemann's types.

f) Three incomplete cranidia from locality 7 have characters displayed by the holotype and two other specimens from locality 16.

This variation suggests that all the known material from Virginia (with the possible exception of the incomplete cephalon from near Tenth Legion) may be included in one species group, the central characters of which are displayed by the holotype here selected. In other specimens, and in by no means the largest known, I_5 is partially developed, rarely complete, and in some cases E_3 is incompletely represented. The development of I_5 suggests that *T. sagenosus* is related to *T. reticulatus* from New York, and one specimen from Virginia seems indistinguishable from *T. reticulatus*.

Tretaspis canadensis Stäuble (1953, pp. 202-210, figs. 17-20), from the Middle Ordovician Quebec City formation, differs from *T. sagenosus* in the more rectangular outline of the cephalon, the more swollen and longer (sag.) cheek roll, the steeply sloping brim, and the presence of a complete I_5 and an incomplete I_6. Stäuble (1953, p. 213) has distinguished his species from *T. kiaeri* Størmer, 1930, and it should be added that in *T. kiaeri* I_6 is only partially developed in relatively few specimens. This means that *T. kiaeri* approaches in many respects some of the specimens from Virginia.

Development

Protaspis. Smallest examples (Pl. 26, figs. 2, 3, 5, 6, 8, 9, 11, 12, 17) of maximum width about 0.4 mm., axis extending entire length, highest at one-third to one-half the length, sides flattened and steeply sloping, steep anterior slope, more gradual backward slope medially and an abrupt slope down in the most posterior part. Pleural regions gently convex, widest just behind the midpoint, tapering forward to give a rounded outline, posterior part narrowing more rapidly back, steep posterolateral and posterior slopes. Three pairs of long slim spines arise from the margins, one anterolateral, one at the greatest width, directed outward and slightly backward, a posterior pair situated close together and backwardly directed. A narrow doublure extends around the posterior half of the shield, reaching forward to a point beneath the bases of the lateral spines; lateral and anterior boundaries of anterior half of shield sutural, the suture curved inward very slightly along the lateral boundary. External surface granulate (what appear to be irregularly scattered short spines are small particles of quartz adhering to the specimens).

Larger protaspides (Pl. 26, figs. 10, 13) are similar in outline and retain the three pairs of border spines. Axis now divided by a faint ring furrow into a longer (sag.) cephalic portion which expands slightly forward, is rounded anteriorly, and much more strongly convex, with a marked keel, this keel extending back a short distance across the ring furrow; the protopygidial portion of the axis is convex, rounded posteriorly, and is slightly wider than the basal part of the glabella. Course of suture, and doublure, similar to that in smaller specimens.

Two protaspides occur in the material from locality 4 which seem by elimination to be those of either a raphiophorid or a trinucleid. That described above has been referred to *Tretaspis sagenosus* n.sp. because of its general similarity in form (apart from the anterolateral and lateral border spines) to that of *Cryptolithus tesselatus* (Pl. 23, figs. 11-16), and because the outline of the glabella, the strong backwardly projecting glabellar keel, and form of the protopygidial portion are like the smallest meraspides of *Tretaspis sagenosus* n.sp. (Pl. 27, figs. 1-3, 7, 14, 15).

Degree 0. One specimen of this degree (now unfortunately lost), had a cranidium alike in size and form to the original of Plate 27, figures 4-6, 10. Still smaller cranidia occur at localities 3 and 4 (Pl. 27, figs. 1-3, 7; maximum width 1.1 mm.). Outline of these is subpentagonal with an almost transverse anterior margin, anterolateral margin running inward and forward and making an acute angle with the posterior margin. Glabella expanding forward, strongly convex, carinate, steeply sloping flat sides, the carina projecting posteriorly behind the rest of the cranidium; median glabellar tubercle situated slightly in advance of the midlength. Axial furrow broad and shallow. Ala a vaguely defined gently convex area, subtriangular in outline, length (exs.) about half that of the glabella. Cheek lobe gently convex, deep pit in posterolateral angle which is continued inward a short distance by a faint furrow; proximally the posterior border is not defined. Sutural margin anterolaterally having a slight inward curvature.

Larger degree 0 cranidia (Pl. 27, figs. 4-6, 10) have a similarly shaped glabella except that the occipital ring is now defined by a shallow occipital furrow and projects slightly posteriorly. Axial furrow broad and shallow, deep anterior pit. Cheek lobes convex, these and the narrow preglabellar field having a gently sloping marginal flange which is the upper lamella of the fringe; this flange is broadest laterally and forms a triangular projection, situated a short distance in front of the projection made by the distal part of the posterior border. Latter now clearly defined by a border furrow. Ala relatively large, triangular, reaching forward to about half the length of the glabella, gently convex and lying below the level of the adjacent part of the cheek lobe. On the cheek lobe immediately in front of the ala is a low ridge directed outward and backward from the axial furrow; this is the eye ridge, but the eye tubercle is not yet defined.

The three smallest examples of isolated transitory pygidia (Pl. 27, figs. 14, 15, 17, 18, 21, 23), all seem by their size to belong to degree 0. Outline transverse, straight anterior margin, lateral margin straight and backwardly converging in the smallest specimens, changing with increasing size to an outwardly convex curve, posterior margin with a slight median notch. Axis convex, not tapering but broadly rounded posteriorly and merging into the pleural regions which are bent down behind the axis. The articulating half ring and two ring furrows are defined on the axis, and on the pleural regions the second and third pleural furrows become evident as short, faint depressions; pleural regions with narrow, sharply raised rim and narrow vertical border.

Degree 1. One complete enrolled exoskeleton (Pl. 27, figs. 8, 9, 11, 12), as well as isolated cephala (Pl. 27, figs. 13, 16, 19), cranidia and pygidia, are known. Glabella clavate, maximum height in advance of half the length, surmounted by median glabellar tubercle; occipital ring wider, curved to project back, occipital furrow shallow medially, deep distally. Ala now relatively narrower, convex and extending forward to a point about opposite half the length of the glabella. Broad eye ridge runs outward and slightly backward from the axial furrow to the highest point on the cheek lobe, where it expands slightly. Posterior border well defined, expanding distally and projecting back just where it joins the internal rim of the fringe. Fringe with broad external rim separated from the cheek lobes anteriorly and anterolaterally by a narrow trough; laterally this narrow trough widens to a triangular region between cheek lobe and external rim; external and internal rims merge into base of long, curving genal spine. In some specimens (Pl. 27, figs. 11, 12) pits are vaguely defined, in others (Pl. 27, figs. 13, 19) there is a double row of pits close together anteriorly and anterolaterally; laterally these two rows diverge to run along each edge of the depressed triangular region, and there are one or two additional pits scattered between them; 20 or 21 pits in the external row on each side. Lower lamella includes a broad external rim, a narrow depression in which the pits are situated, and an inner, rolled margin which is smoothly curved and has a slight median backward projection. Posteriorly the suture runs along internal rim, curves across the genal angle and runs forward along the upper, outer edge of the external rim.

The single thoracic segment is cut off diagonally where it fits beneath the bent-down outermost part of the posterior cephalic border. Transitory pygidium (Pl. 27, figs. 20, 22) now with lateral margins curving inward and backward, slight median notch in margin of border. Axis gently convex, not sharply defined by axial furrows; first and second axial rings narrow (sag.), convex, deep articulating and ring furrows. Three narrow and deep pleural furrows, the first extending out to the rim, the second and third successively shorter and more backwardly directed. Pleural regions not bent down so strongly behind the axis.

Larger meraspides and holaspides. Cephala of width slightly less than 3 mm. (Pl. 28, figs. 1-4), which must be of at least degree 3, are similar in form to those of degree 1. The glabella is slightly less convex longitudinally and does not bulge forward to overhang the fringe: cheek lobe and ala similar, the eye ridge broad and backwardly directed, the eye tubercle distinct and situated on the edge of the outer slope of the cheek lobe. Fringe is much broader, sloping gently outward and downward, the rims proportionally narrower, the pitted portion proportionally broader and not in a deep furrow. There are three complete rows of pits anteriorly and anterolaterally; laterally the inner and outer of these rows is continuous and between them are scattered and irregularly arranged pits. On the lower lamella the girder is present as a low ridge running inside the outermost row of pits and continuing onto the inner, lower angle of the genal spine. The reticulate pattern of raised ridges is present on the cheek lobe, and raised lines run along the external rim of the fringe and continue on to the genal spine. With the expansion of the fringe the prolongation also begins to develop, and the genal angle is now behind the posterior cephalic border.

Next largest cephalon (Pl. 28, figs. 5-8) of width 3.4 mm., frontal lobe of glabella relatively wider but glabella still sharply carinate, with the basal and median glabellar furrows now defined. Ala narrower and reduced in length, convex and posteriorly merging into the junction of the occipital ring and posterior border. Eye tubercle situated on edge of outer slope of cheek lobe and about opposite median glabellar furrow, eye ridge narrow adjacent to eye tubercle, becoming broader as it approaches and crosses the axial furrow. Reticulate pattern of raised lines now well developed on the median parts of glabella and cheek lobes. Fringe broader and sloping gently outward, five rows of pits anteriorly and anterolaterally, additional pits laterally; girder more prominent and separating the external two rows from the inner rows; 26 or 27 pits on each side in E_1 and E_2; on upper lamella low concentric ridge now separates I_1 from I_2. The cranidium of width about 6 mm. (Pl. 26, fig. 1) has assumed the essential characters of the largest specimens. The glabella now has the frontal lobe rounded in dorsal aspect and no longer carinate in anterior view, but gently rounded; the occiput and the basal and median glabellar furrows are well developed, the anterior glabellar furrow faint. Ala much reduced but visible as a distinct swelling in the broad axial furrow; eye ridge broad where it crosses this furrow. Fringe now with cheek roll more steeply sloping than the brim, the full complement of pits and the concentric ridges on the upper lamella separating I_1 to I_4.

Pygidia larger than those of degree 1 (Pl. 27, figs. 24, 25; Pl. 24, figs. 10, 13) show the axis becoming better defined, divided into at least five rings and tapering backward; pleural regions horizontal, three or four pairs of pleural furrows, and in transitory pygidia interpleural grooves may be observed (Pl. 27, fig. 24). The outer parts of the pleurae are bent steeply down and in posterior view the margin shows the shallow median notch.

Family RAPHIOPHORIDAE Angelin, 1854

Earlier diagnoses (Whittington, 1950b, p. 552; 1959, p. O426) now need emendation, in that the ala may, or may not, be united at the inner posterior corner to the extremity of the occipital ring, and the hypostome, the generalized characters of which are discussed below, is now known.

General Characters of *Ampyx, Lonchodomas, Ampyxina* and *Raymondella*

Holaspid Morphology

Cephalon (Pl. 29; Pl. 32, figs. 1-9, 12, 16, 17, 20; Pl. 34, figs. 3-17, 22; Pl. 36, figs. 1-7). The forwardly expanding glabella and variably developed frontal spine are characteristic. In all the species discussed here the occipital ring lacks a doublure. Occipital furrow variable in depth, distal part most pronounced. In *Ampyx* (Pl. 29, figs. 2-4) and *Lonchodomas* (Pl. 32, fig. 23) muscle areas are visible in the outer part of this furrow. The lateral glabellar furrows are not developed as narrow, deep troughs, but rather as subcircular or suboval areas which may be slightly depressed in the external surface. The exoskeleton is thinner over these areas and in many specimens appears of a different color, or because of its thinness may be broken through (Pl. 34, fig. 3). These areas have been referred to as muscle areas, since in the silicified material this is what they seem to be (cf. Whittington and Evitt, 1954, pp. 24-25). Three pairs of muscle areas in front of the occipital furrow have been observed in *Ampyx, Lonchodomas,* and *Ampyxina,* in *Raymondella* one pair. The pair common to all these genera is the basal or preoccipital, and is generally impressed into the outer surface and in, for example, *Ampyxina* (Pl. 34, figs. 3, 15) and *Raymondella* (Pl. 36, fig. 2) gives a pinched-in appearance to the basal part of the glabella. The second of these muscle areas is about half way up the steeply sloping side of the glabella in *Ampyx* (Pl. 29, figs. 2, 3) and *Lonchodomas* (Pl. 33, figs. 31, 32), the third close to the anterior pits in these genera, but in *Ampyxina lanceola* (Pl. 35, fig. 32) it is a short distance inside the axial furrow.

In *Ampyx* (Pl. 29, figs. 1-3) there is an elongate, narrow (tr.), gently convex portion of the glabella between the axial furrow and the outer edges of the first two muscle areas which extends forward to the third (anterior) muscle area. The corresponding region in the glabella of *Ampyx linleyensis* Whittard (1955, pp. 18-21, pl. 2, figs. 1-5) has been described by Whittard as the ala. It seems to me more likely, in view of the developmental series described here, that this region is part of the true glabella, i.e., it is within the axial furrow in *Ampyx linleyensis* as it is in *A. virginiensis*.

Cheek is convex, subtriangular in outline, with a well defined posterior border, the posterior border furrow running distally into a deep pit. Lateral and anterior borders are narrow, well defined in *Ampyx*, *Ampyxina*, and *Raymondella*. The anterior border furrow is weak or absent on the fixed and free cheeks adjacent to the suture line (Pl. 29, figs. 5, 6; Pl. 34, figs. 14, 17; Pl. 36, figs. 4, 5). In *Lonchodomas* anterior and lateral cephalic borders of comparable width are not outlined by border furrows (Pl. 32, figs. 1, 7). Facial sutures have a characteristic course, commencing on the posterior border a short distance in from the genal angle, curving outside the pit in the posterior border furrow, then running across the lateral part of the cheek in a curve concave outward, and meeting along the anterior and anterolateral margins of the cephalon. There is no trace of median or connective sutures, as some of the more complete specimens show (Pl. 29, figs. 5, 6; Pl. 32, figs. 2, 3; Pl. 34, figs. 7, 8; Pl. 36, figs. 1-4). The librigenal spine arises from the genal angle and the upper part of it merges into the upper surface of the cheek at the genal angle. Librigenal spines are at first outwardly and backwardly directed and may curve to point backward and extend for a lesser or greater distance beyond the pygidium. *Lonchodomas carinatus* (Pl. 32, figs. 4, 5; Text-fig. 8) is most unusual in the hooked form of the genal spine, but even so, if the restoration is correct, the tip of the spine extends just beyond the pygidium.

The hypostomes of *Ampyx* (Pl. 29, figs. 9, 10, 12-16), *Lonchodomas* (Pl. 32, figs. 6, 8, 9, 12, 17) and *Ampyxina* (Pl. 34, figs. 5, 9) have the following characters in common: greatest width across anterior wings, anterior margin either curved convexly forward or three sided, lateral borders convergent backward. Middle body convex, anterior border becoming defined along distal part of anterior margin and continuous with lateral and posterior borders. Macula situated on posterolateral part of middle body. Anterior edge rounded, thin, edges of lateral and posterior borders turned up to slope vertically and excavated between wings; no anterior wing process, posterior wings small.

The hypostome has not been found in position. The thin, rounded anterior edge, and the similar inner edge of the anterior part of the cephalic doublure, do not suggest that the hypostome was linked to the cephalic doublure along a hypostomal suture, for along such junctions the edges are usually thick and flat. Further, the curvature of the outline of the anterior margin of the hypostome does not correspond exactly with that of the inner margin of the cephalic doublure. An enrolled specimen of *Ampyx nasutus* (Whittington, 1950b, pl. 74, figs. 5, 6, 8) shows the border of the pygidium lying close against the inner edge of the cephalic doublure, implying that the hypostome could not have been joined to this edge. In *Lonchodomas* (compare Pl. 32, figs. 2, 3, with Pl. 32, figs. 18, 21) the outline of the inner margin of the anterior portion of the cephalic doublure, with its median notch, accurately corresponds in curvature to that of the border of the pygidium. The same may be said of *Ampyxina powelli* (compare Pl. 34, figs. 7, 8 with Pl. 34, figs. 3, 4) and *A. lanceola* (compare Pl. 34, figs. 15, 16 with Pl. 34, figs. 25, 27), and is probably also true of *Raymondella*. It is therefore suggested here that in raphiophorids the hypostome was held close beneath the glabella and that perhaps muscles held the anterior wing close beneath the prominent anterior boss (Text-fig. 8c); during enrollment the border of the pygidium lay against the inner edge of the cephalic doublure. These statements apply equally to *Cryptolithus tesselatus* (Pl. 21, fig. 16; Whittington, 1941b, p. 517, pl. 75, fig. 2).

Thorax of six segments in *Ampyx* (Pl. 30, figs. 1-5), five in *Ampyxina* (Pl. 34, figs. 3, 4), and probably five in *Lonchodomas* and *Raymondella* (Whittington, 1950b, p. 557-58); axis relatively narrow, pleurae and pleural regions horizontally extended, only the outermost parts bent down steeply or vertically, doublure narrow and tightly curled under (Pl. 30, figs. 6-13; Pl. 32, figs. 10-15; Pl. 34, figs. 18-20; Pl. 36, figs. 24-26, 29-32). The outer parts of the thoracic pleurae become longer (tr.) in successively posterior segments, the anterolateral edge of the first segment is cut off where it fits against the cephalon, facets on the succeeding segments fit into recesses in the doublure during enrollment. Pleural furrows well defined.

Pygidium (Pl. 30, figs. 14, 16, 17, 20; Pl. 32, figs. 18, 19, 21, 22; Pl. 34, figs. 25-27; Pl. 36, figs. 33, 34, 37) with axis tapering back to rim, eight or nine segmental divisions indicated by ring furrows or muscle areas in *Ampyx, Lonchodomas* (cf. Størmer, 1949, p. 178, fig. 146) and *Ampyxina*, four in *Raymondella*. Inner part of pleural region flat, variably furrowed, outer part forms a broad vertical border, the margin of this border characteristically sinuous in outline, with a median posterior notch.

External surface smooth or finely granulate, anastomosing raised lines on cheek of *Raymondella*, raised lines running subparallel to the margins on the cephalic, including hypostomal, borders and on the outer parts of the thoracic pleurae and pleural regions of the pygidium.

Development

Protaspis. A protaspis here attributed to *Ampyx* (Pl. 30, figs. 21-30) is the only one known among raphiophorids. Axis is broad, subparallel sided, most convex in the cephalic portion. Pleural regions slope steeply laterally and behind the axis. Free cheeks and hypostome not known, the cranidial portion being bounded by the facial suture, which has a scalloped outline, including a gentle curve concave outward along the anterolateral margin. In the smaller specimen the suture curves across the doublure at about half the length (Pl. 30, fig. 30); in a larger specimen (Pl. 30, fig. 22) the suture crosses the doublure much farther backward, at about four-fifths the length, in a curve that is sharply convex backward so that a tiny projection is isolated on the inner part of the doublure. Two pairs of marginal spines, one anterolateral, the other posterior; between the posterior pair the margin is deeply notched in posterior view (Pl. 30, fig. 27) and the doublure of this notch bears a tiny pair of downwardly and inwardly directed spines. In its general form, and in such details as the course of the suture across the doublure and the posterior notch with its ventrally directed spines, this protaspis is remarkably like that of *Cryptolithus* (Pl. 23, figs. 11-16). It is similar to, but less strikingly like, the protaspis of *Tretaspis* (Pl. 26, figs. 2, 3, 5, 6, 8-13, 17).

Meraspides. Early meraspid degrees are known of at least some species of all the genera here considered. The only example of a degree 0 exoskeleton is one questionably attributed to *Ampyx* (Pl. 31, figs. 1, 2). This latter suggests that the two pairs of border spines of the supposed protaspis are reduced, and lost abruptly, between the protaspis and onset of the meraspid degrees. At the same time, the frontal glabellar spine, which is not present in the protaspis, appears abruptly at degree 0. This phenomenon of the abrupt disappearance and/or appearance of spines between the protaspid and early meraspid degrees is paralleled in the development of quite unrelated trilobites — for example Remopleurididae, or Odontopleuridae (Whittington, 1956).

The earliest developmental stages of *Ampyx* (Pl. 31, figs. 3-5, 21, 22), *Ampyxina* (Pl. 35, figs. 1-3, 5, 6, 10, 11), *Lonchodomas* (Pl. 33, figs. 1-3, 4, 7), and *Raymondella* (Pl. 36, figs. 18, 19, 22, 23, 27, 28) show a family resemblance to one another — in the clavate, keeled form of the glabella with its frontal spine, outline of the cheeks and faintness of the posterior border furrow, development of the alae (except in *Lonchodomas*), and form of the transitory pygidium with its axis expanded posteriorly and the posterior part of the pleural regions bent down sharply, the pleural regions having a narrow raised rim. Nevertheless, generic characters such as the cranidial outline and carinate glabella of *Lonchodomas*, and the constriction in the pre-occipital part of the glabella of *Ampyxina* and *Raymondella*, are apparent at this stage. These latter two genera are alike at degree 2 (compare Pl. 35, figs. 5, 6, 10, 11 with Pl. 36, figs. 18, 19, 22, 23), the inflation of the anterior part of the glabella of *Raymondella* — a generic character — taking place after this stage. The development of the hooked shape of the librigenal spine of *Lonchodomas* takes place in the later meraspid degrees (Pl. 33, figs. 11, 16). Some developmental features are common to all — increase in convexity of the glabella, deepening of the posterior border furrow of the cephalon, flattening out of the pleural regions of the pygidium and development of the steep pygidial border. Other morphological features such as the keel of the glabella or the frontal glabellar spine may be progressively augmented (*Ampyx* and *Lonchodomas*), or reduced almost to disappearance (*Ampyxina, Raymondella*) in the largest individuals. Alae are barely discernible in the supposed late protaspis (Pl. 30, fig. 29) and degree 0 (Pl. 31, figs. 1, 2) of *Ampyx*, but are clearly visible at about degree 2 of *Ampyx* (Pl. 31, figs. 3, 7), *Ampyxina* (Pl. 35, fig. 5), and *Raymondella* (Pl. 36, fig. 16). At this stage they are triangular areas enclosed between the axial and alar furrows, gently convex, and posteriorly weakly separated from the border, the inner posterior corner merging into the extremity of the occipital ring. Alae are not present at any known stage of *Lonchodomas*. In the later development of the genera in which they are present, they may be progressively reduced and disappear in the holaspis (*Ampyx*), or be retained (*Ampyxina, Raymondella*). In *Raymondella* (Pl. 36, figs. 1, 2) the convex portion is separated from the posterior border and occipital ring by a depression, but in *Ampyxina* (Pl. 34, figs. 3, 15, 16) the inner posterior corner is connected to the extremity of the occipital ring. From the evidence reviewed here it seems reasonable to conclude that the alae are not part of the glabella, though they seem to be closely connected to the basal part of it. Alae are present in the development of species of the closely related family Trinucleidae, are similar in appearance to those of raphiophorids, and in some species appear to be retained in the holaspis (Whittard, 1955, pp. 32, 36). Størmer (1930, p. 65) concluded that the alae of Trinucleidae belonged to the glabella, but in view of what we now know of raphiophorid development this statement may be open to question. No light can be shed on the question of the function of the alae.

Genus AMPYX Dalman, 1827

AMPYX VIRGINIENSIS Cooper, 1953

Plate 29; Plate 30, figures 1-14, 16, 17, 20-30; Plate 31; Text-figure 7

Figured Material. All in USNM

Geological Horizon and Localities. Lower part of Edinburg limestone, localities 2, 3, 4, 5, 6, 16.

Description. Reconstruction of exoskeleton (Text-fig. 7) shows outline and convexity; length (sag.) of cephalon almost half that of exoskeleton. Glabella (Pl. 29, figs. 1-4) narrowest across occipital ring; this ring is sharply ridged, with a vertical posterior slope and a steep slope down to occipital furrow, and not separated by a depression at the axial furrow from the posterior border. Posterior, ventral edge of occipital ring thickened, but doublure absent. Occipital furrow broad and shallow, in dorsal aspect both occipital furrow and ring curved convexly backward. Glabella, defined by shallow axial and preglabellar furrows, expands forward to a maximum width at about one-third the length, anterior part rounded in dorsal outline, projecting beyond

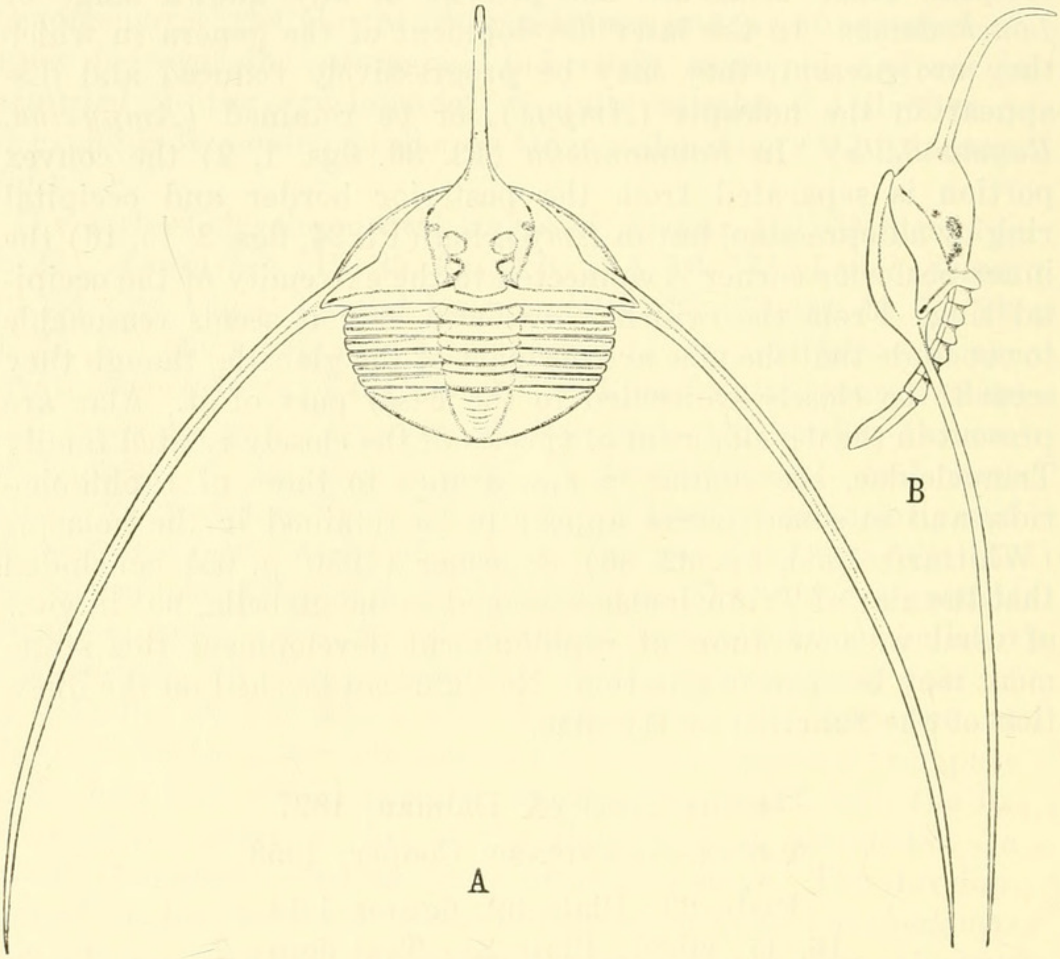


Figure 7. *Ampyx virginiensis* Cooper, 1953. Reconstruction, A, dorsal, B, left lateral views. Approximately X 2.

cephalic margin, and drawn out into long, curved spine, the tip of which is directed upward and slightly backward; glabellar spine round in section, longitudinal lateral furrow in proximal portion; behind base of spine glabella rounded (not carinate) along midline, sides flattened and steeply sloping. Four pairs of muscle areas (visible by their colour, the thinness of the exoskeleton over them, or by being impressed): occipital area elongate-oval, situated in outer part of occipital furrow, adjacent to it is subcircular first lateral scar, the anterior, inner and posterior boundaries of which are impressed into glabella, and the outer, posterior corner connected by a shallow depression to the occipital area; second lateral area larger, subcircular in outline, situated immediately in front of first and half way up slope of glabella, not impressed; third lateral area smaller, subcircular in outline, adjacent to axial furrow and at greatest width of glabella. In axial furrow, adjacent to posterior border furrow, there is a narrow (tr.), short (exs.) depression, probably a muscle area; anterior pit deep, elongate, situated in front of third lateral muscle area.

Cheek (Pl. 29, figs. 5-8, 11) gently convex, lateral and anterior border narrow, flattened, defined by change in slope rather than a furrow; border flexed down at margin and rolled under to form a doublure which is no wider than the border; anterior border and preglabellar furrows coincident. Posterior border a sharp ridge, anteriorly sloping to broad shallow posterior border furrow, latter with deep pit distally; distal part of border bent down; on posterior edge, just inside suture, is a socket to receive anterolateral corner of first thoracic segment. Facial suture cuts posterior margin near extremity of border, from here runs outward and slightly forward, curves abruptly back over posterior border furrow outside distal pit, follows a gently sinuous course across outer part of cheek, and two branches meet in smooth curve along anterior margin of border. No median or connective sutures. Librigenal spine long and gently curved, base formed by extensions of lateral and posterior cephalic borders; posterior border furrow of cephalon is continuous with shallow longitudinal furrow on upper surface of librigenal spine, similar furrow on lower surface of spine so that, proximally, cross-section is hour-glass shaped; furrows die out distally; an elongate depression on inner side of spine near base. Anterolateral and anterior parts of cephalic doublure divided by a flexure into an outer, wider, flat part and an inner, gently convex part; flexure has a slightly sinuous course; inner edge of doublure thick, rounded, traversed by fine raised lines.

Hypostome (Pl. 29, figs. 9, 10, 12-16) shield-shaped, anterior margin gently curved convexly forward, medially no anterior border; distally a gently convex border becomes defined and is continuous with lateral and posterior borders; shallow border furrow. Middle body most convex in median part, gently sloping anterolaterally; thinner area in anterolateral corner adjacent to border, probably a muscle area; shallow pit in border furrow posterolaterally. In lateral and posterior views (Pl. 29, figs. 14, 15) border is seen to be deepest (i.e. extended dorsally but not curled inward) laterally and posteriorly, and outline shows a lateral and median posterior scallop, with a long, pointed postero-lateral projection (the posterior wing) between the scallops.

Thorax (Pl. 30, figs. 1-13) of six segments, first the longest (sag. and exs.), succeeding segments progressively shorter, and, after the second, narrower (tr.); axis gently convex, one-third of total width and tapering slightly. Subcircular distal part of axial ring gently inflated, posterior edge of ring with slight median indentation; articulating furrow broad and shallow, running in curve concave forward, articulating half-ring and doublure of ring short (sag.); oval area in outer part of articulating furrow is slightly more depressed than rest of furrow and may be different in colour, and is probably a muscle attachment area. Small axial articulating processes and sockets, absent only between first thoracic segment and occipital ring. Inner part of pleura horizontal, outer part of pleura short (tr.), bent down steeply; pleural furrow broad, shallow, directed slightly diagonally, deepening and curving forward as it reaches fulcrum and ends against facet; in dorsal aspect line of fulcrum is inward and forward on first segment, on succeeding segments progressively more strongly inwardly and backwardly directed, giving characteristic outline to thorax; in addition outer part of pleura is longer (tr.) on succeeding segments (compare Pl. 30, fig. 6 with Pl. 30, fig. 8). Fulcral articulating process and socket on each segment, including process on first segment which fits into socket in posterior border of cephalon where latter is flexed downward. Doublure of pleura short (tr.), curled under outermost part of pleura; each pleura with small facet on outer part, the tip of the facet being received during enrollment by a depression in the doublure of the preceding segment, this mechanism providing a limit to amount of enrollment.

Pygidium (Pl. 30, figs. 14, 16, 17, 20) three times as wide as long, gently convex axis tapering back to reach inner margin of border. Articulating furrow with deeper outer part, short (sag.) articulating half-ring. Eight or nine axial rings indicated by furrows which are deepest medially and become progressively fainter posteriorly. In outer part of each furrow an oval muscle area, corresponding in position with deeper part of articulating furrows of pygidium and thorax. Inner part of pleural region horizontal, crossed by broad pleural furrow running in curve concave forward; area in front of this furrow bent to slope upward and forward, most strongly bent distally adjacent to articulating process and inner part of facet. Border slopes steeply and is broad, edge curled under and in posterior view with a characteristic bow-shaped outline imposed by the greatest width being posterolateral and by the median posterior notch.

External surface smooth (or extremely finely granulate) but not "punctate" as stated by Cooper (1953, p. 16), fine granulation on glabellar spine (Pl. 29, figs. 1, 3) and on proximal part of librigenal spine, fine raised lines on outer part of cephalic border, border of hypostome, and outer part of pleural regions of thorax and pygidium, these lines running subparallel to the margins.

Discussion. *Ampyx virginiensis* is extremely like the type species *A. nasutus* (Whittington, 1950b, pp. 554-556, pl. 74, figs. 3-9, text-fig. 6) from the Lower Ordovician of Sweden, differing only in such features as the less forwardly projecting glabella, narrower anterior and lateral cephalic border and relatively shorter pygidium.

Cooper (1953, pp. 16-17, pl. 7, figs. 1-11, 18) erected this species for material from the present localities 2 and 6. The relatively longer (sag.) pygidium, with deeper axial furrows, of *Ampyx americanus* (Cooper, 1953, pl. 5, figs. 3-5, 8, 9 [figure 3 is X2, not X5 as stated by Cooper]), from a similar horizon in Tennessee, serves to distinguish it from *A. virginiensis*. *A. camurus* (Cooper, 1953, p. 16, pl. 5, figs. 1, 2, 6, 7; this paper, Pl. 30, figs. 15, 18, 19), is distinguished from *A. virginiensis* by the more convex frontal portion of the glabella and the relatively longer pygidium which has a more triangular outline. Both species occur at about the same horizon in Virginia, but *A. camurus* has not been found among the silicified material. From the same locality and horizon that yielded *A. camurus* came also *A. lobatus* Cooper, 1953 (p. 16, pl. 6, figs. 3, 4), based on a distinctive pygidium that exhibits the second and third pleural furrows extending across the inner pleural regions. Comparable furrows are not present on pygidia of *A. virginiensis* of the same size. I have not seen the type material of *Ampyx? hastatus* Ruedemann (1901, pp. 48-54, pl. 3, figs. 1-10, 30), but it appears to differ from *A. virginiensis* in the presence of the carina on the glabella, the prismatic section of the frontal glabellar spine, and outline of the pygidium. *A. virginiensis* has one, rather than two, anterior glabellar muscle scars.

Whittard (1955, p. 19, pl. 2, fig. 8) has described the hypostome of *Ampyx linleyensis*. That of *A. virginiensis* is similar, but wider (tr.) across the anterior wings, the position of which is revealed by the muscle area. Whittard interprets the projection bounding the anterior margin of the notch in the lateral border as the anterior wing in *A. linleyensis,* but by analogy with *A. virginiensis* the anterior wing may be in advance of this position.

Development

Protaspis. The protaspis here attributed to *A. virginiensis* occurs at localities 3 and 4, where small developmental stages of the species are quite abundant. This protaspis does not seem to be that of *Lonchodomas carinatus* since small developmental stages of this species are rare at locality 3, and do not occur at locality 4.

Smallest specimen (Pl. 30, figs. 26, 30) of length (sag.) 0.47 mm., maximum width 0.49 mm. Greatest width at about half the length, in front of which straight lateral margins converge slightly forward to the obliquely angulate anterolateral margin; anterior margin curved gently forward; behind greatest width shield narrows more rapidly and is rounded. Axis of width about one-third that of entire exoskeleton, subparallel sided and rounded at each end. Pleural regions curved down more steeply posterolaterally, almost vertical behind the axis; at anterolateral angle a long slim spine, a second spine on the posterior margin in line with the axial furrow; between posterior pair of spines margin is notched. Doublure narrow, extending forward to about the maximum width; in front of this point margin of the exoskeleton is sutural. Free cheeks unknown.

A slightly larger example (Pl. 30, figs. 21-24, 27; length 0.53 mm.) is similar in form but has the axis divided by a ring furrow; glabellar portion more strongly convex at the rounded anterior end, protopygidial portion more convex and slightly wider than the basal part of the glabellar portion. Posterior margin of protopygidium deeply notched between bases of spines, doublure of notch bearing a short, ventrally and inwardly directed spine on each side. Doublure extends forward only a short distance in front of posterior spine before being cut off by suture — apparently the suture in this specimen extends farther back than in the smaller one, and therefore anterior margin of pleural region of protopygidium must run outward and backward from base of glabella. Free cheek unknown.

The largest example (Pl. 30, figs. 25, 28, 29) is incomplete and apparently has the border spines broken off; it is similar in form but the glabella has a definitely clavate outline and is narrower across the basal part than across the expanded, convex, anterior part. Faint transverse furrow extends across pleural regions to divide cephalic from protopygidial portion; thus anterior margin of protopygidium is transverse and pleural region is longer (exs.) and wider.

Degree 0. Ampyx virginiensis is rare at locality 16, yet one specimen (Pl. 31, figs. 1, 2) is a degree 0 raphiophorid, and seemingly belongs to this species. Glabella now outlined by shallow axial furrows, sloping steeply posteriorly to the narrow (sag. and exs.), faintly defined occipital ring, anteriorly projecting forward over the cephalic margin (the outline of which is concave medially) and continued by a thick, forwardly directed glabellar spine; shallow depression in side of glabella immediately in front of occipital ring. Fixed cheek gently convex, sloping steeply anterolaterally, bent down along posterior margin but the posterior border not defined. Fixed cheeks united in front of glabella by narrow (sag.) preglabellar area. Fixed cheeks and preglabellar area bounded by facial suture, which on the left side has the characteristic slight inward curvature, and continues around the posterolateral corner. Free cheeks and hypostome unknown. Transitory pygidium more than twice as wide as long, curved down (sag. and exs.) so that posterior part slopes vertically; axis stands above pleural regions, divided by shallow ring furrows into two gently convex rings and a more convex terminal portion; pleural region flat in a transverse direction, narrow raised rim, narrow border curled under as a narrow doublure.

Cephalon. Smallest cranidium (Pl. 31, figs. 3-5; length excluding glabellar spine 0.3 mm., maximum width 0.69 mm.; length glabellar spine 0.49 mm.) subsemicircular in outline, ovoid glabella with rounded median ridge and steeply sloping sides, deep, round pit immediately in front of distal part of low occipital ring, glabellar spine long, round in section, curved slightly down in lateral view. Ala occupies inner one-third of area of cheek, is gently convex, outlined by shallow alar and axial furrows. Posterior border faintly indicated distally by depression. Facial suture curves around posterolateral corner of fixed cheek and course is faintly indented in lateral margin.

Next largest cranidium (Pl. 31, figs. 7-9; length excluding glabellar spine 0.45 mm., maximum width 0.94 mm.) has anteromedian part of glabella higher and more convex so that it projects farther forward, the glabellar spine is straight, ala is more distinctly outlined, and posterior border furrow is complete, ending distally in a pit. Free cheek shows the lateral and anterior borders and border furrows, is relatively narrow (tr.) compared to larger specimens (apparently because of the lesser inward curvature of the suture laterally), and has a backwardly curving librigenal spine. The doublure is narrow.

In cephala up to a length (sag., excluding glabellar spine) of 1.5 mm. (Pl. 31, figs. 6, 10-20) the glabella becomes slightly more convex and the frontal spine upcurved. The depression in front of the occipital ring becomes recognizable as the basal muscle area, and in cephala of length 1.42 mm. or more the second and the anterior areas are visible (Pl. 31, fig. 15). The ala persists as a convex area in the inner corner of the cheek, connected by a low ridge to the extremity of the occipital ring, but becomes progressively smaller. The facial suture curves more strongly inward across the lateral part and the cheek, and the free cheek becomes wider (tr.); the proximal part of the librigenal spine becomes straight and outwardly and backwardly directed. Granulation, present on the external surfaces of cephala of length (sag.) 0.52 mm. (Pl. 31, figs. 6, 10), where it is coarsest on the free cheek, becomes finer. Beyond a length (sag.) of 1.4

mm. there is little change in the cephalon, except that the ala disappears; a trace of it in the form of a low ridge connecting the inner corner of the cheek to the extremity of the axial ring is visible in cephala of length 3 mm. and slightly larger. The smallest known hypostomes do not differ greatly from the largest.

A size series of transitory and true pygidia, believed to be that of *Ampyx virginiensis*, is shown in Plate 31, figures 21-32. The corresponding series of *Lonchodomas carinatus* (Pl. 33, figs. 7, 10, 13, 15, 18, 20, 21, 25) is quite similar, especially at the smaller sizes, and such transitory pygidia of these two species are not readily separated. Pygidia of length (sag.) 0.69 mm. (Pl. 31, figs. 31, 32) of *A. virginiensis* differ from larger examples (Pl. 30, figs. 14, 16, 17, 20) in the presence of the second, third, and faint fourth pleural furrows (each one directed more strongly backward), in showing faint interpleural grooves, and in possessing the rim. Following the series through progressively smaller sizes, the convex axial rings become more clearly defined by ring furrows having a distal pit, the outline becomes more rounded, the border narrower and the rim stronger. In the two smallest specimens (Pl. 31, figs. 21-24) a posterior indentation appears, and in the smallest of these only two axial rings and a bulbous terminal portion are visible, and the pleural regions are bent down posteriorly. The characteristic bow-shaped outline of the external margin of the border, seen in posterior view, is present throughout the series. This smallest transitory pygidium (Pl. 31, figs. 21, 22) is larger than that of the degree 0 specimen (Pl. 31, figs. 1, 2), and differs in exhibiting pleural furrows and a more acute angle between the outline of the anterior and lateral margins.

Genus LONCHODOMAS Angelin, 1854

LONCHODOMAS CARINATUS Cooper, 1953

Plates 32, 33; Text-figure 8

Figured Material. All in USNM

Geological Horizon and Localities. Lower Edinburg limestone, localities 2, 3, 5, 6, and Willow Grove, 3 miles south of Woodstock, Shenandoah Co., Virginia.

Description. Cephalon (Pl. 32, figs. 1, 4, 5, 7) excluding spines triangular in outline, about twice as wide as long. Glabella subdiamond-shaped in outline; occipital ring a narrow (sag.) band, not separated by axial furrow from posterior border and not raised above the adjacent part of the border, posterior margin gently arcuate backward; occipital furrow extremely shallow; in front of this furrow glabella becomes moderately convex, with a median longitudinal carina from which the gently convex sides slope steeply down, maximum width in front of the mid-length, anterior part drawn out into a long, tapering, frontal glabellar spine which is directed horizontally with an extremely slight upward curvature, the spine square in cross section, each corner of the square projecting slightly to form a longitudinal ridge, the two ridges on the upper surface running back to join and merge into the carina, the two ridges on the lower surface being continuous with the anterolateral edge of the cephalon; muscle areas on the glabella (darker areas, smooth externally — Pl. 32, fig. 23; Pl. 33, figs. 31, 32; Text-fig. 8a) include a small oval area in the distal part of the occipital furrow, in front of this a subtriangular area, the posterior part of which extends up the side of the glabella quite close to the carina, confluent with this a third elongate-oval area disposed longitudinally on the glabella about half way up the slope; a fourth poorly defined area is situated on the slope of the glabella just inside the anterior pit. The anterior area was not observed in *Lonchodomas rostratus* (Whittington, 1950b, fig. 7) but may be seen in *Lonchodomas* sp. of Størmer (1949, p. 178, fig. 14b). There seems no evidence for the subdivision of the basal and median areas shown by Hupé (1953, p. 72, fig. 26, *3*). Axial furrows not distinct, limits of glabella ill-defined by change in slope and by the deep elongate anterior pit which is situated opposite the maximum width of the glabella.

Cheek subtriangular in outline, sloping anterolaterally, inner part gently convex, outer part sloping less steeply towards the acutely angulate margin (Pl. 32, fig. 1) so that in profile there is a gentle concavity; posterior border sloping steeply forward, posterior border furrow commencing a short distance outside the occipital ring and ending just inside the facial suture in a deep pit; at about half its width the posterior border is bent down to slope gently outward; librigenal spine thick, hook-shaped, ending in a sharp point, prismatic in cross section, each edge raised to form a strong ridge, the surfaces between the ridges concave.

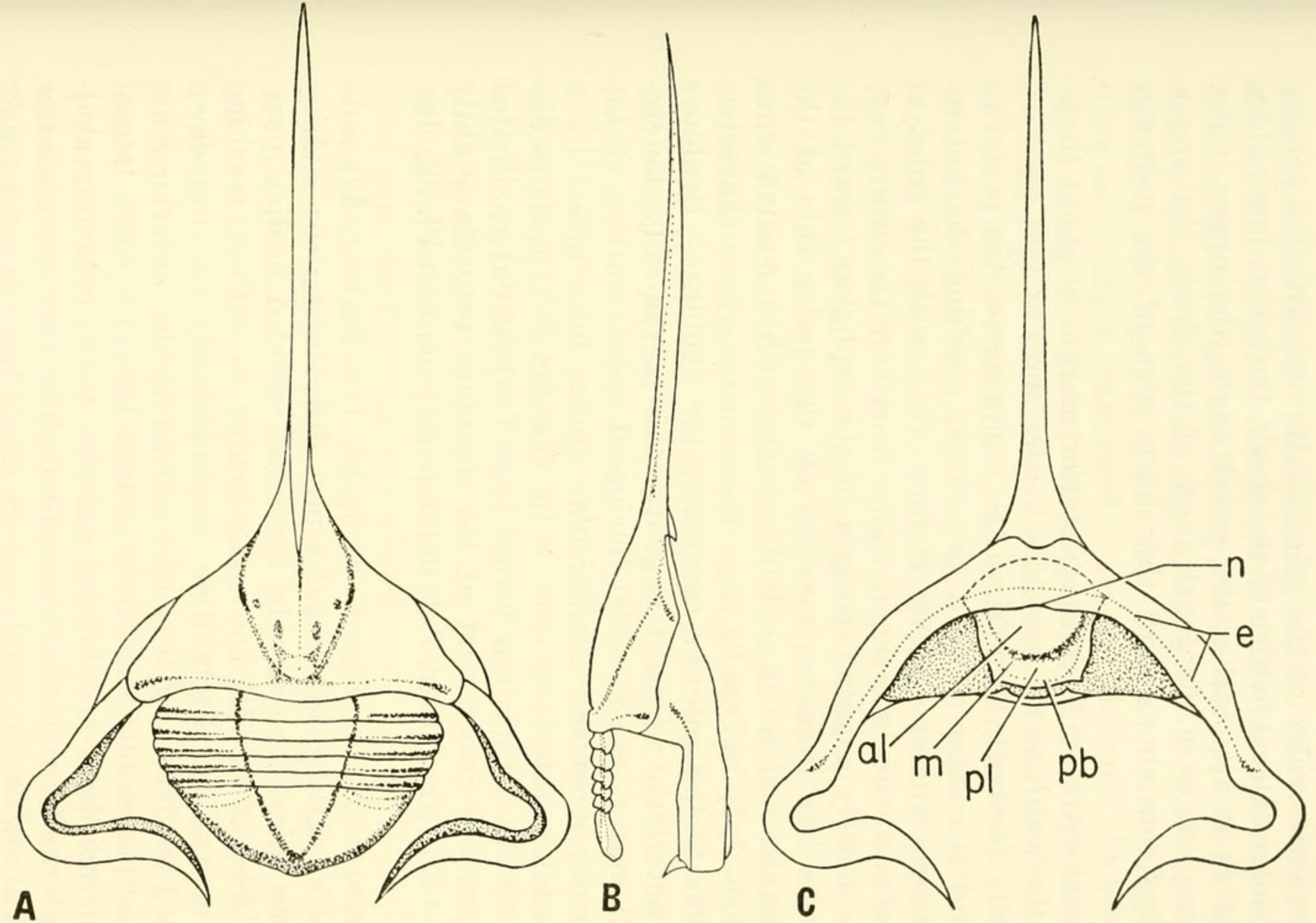


Figure 8. *Lonchodomas carinatus* Cooper, 1953. Reconstructions, A, dorsal, B, right lateral, C, ventral views. Approximately X 2½. Abbreviations: *al*, anterior lobe of middle body of hypostome; *e*, edge of elevated inner part of cephalic doublure; *m*, macula; *n*, notch in inner margin of cephalic doublure; *pb*, posterior border of hypostome; *pl*, posterior lobe of middle body of hypostome.

The lower, outer ridge of the spine continuous with the acutely angulate anterolateral border of the cheek, the lower, inner ridge dying out as it approaches the genal angle, the upper, outer ridge dying out over the genal angle of the cheek, the upper, inner ridge continuous with the sharp edge of the posterior border.

The facial suture crosses the posterior margin at about three-quarters the width of the posterior border, runs at first outward and slightly forward, then in an 'S' curve across the posterior border and the outer part of the cheek, reaching the antero-lateral margin almost directly in line (exs.) with the point at which it crossed the posterior margin; from here the suture runs along the acutely angulate margin of the cephalon toward the midline, the two branches meeting on the under side of the frontal glabellar spine in a double curve with a median sinus (Pl. 32, figs. 2, 3, 5; Text-fig. 8c) ; these curves give a characteristic outline to the anterior margin of the doublure. Doublure broadest anteriorly where it is gently convex ventrally, antero-laterally about as wide as the librigenal spine; outline of the inner margin a smooth semicircular curve, interrupted by a shallow median anterior notch (*n* in Text-fig. 8c) ; a short distance inside this margin is a flexure (*e* in Text-fig. 8c) so situated that the narrow inner part of the doublure projects slightly ventrally below the wider, flat, outer part (compare Pl. 32, figs. 2, 3).

Hypostome (Pl. 32, figs. 6, 8, 9, 12, 17; Text-fig. 8c) sub-hexagonal in outline, in ventral aspect flexed along the midline so that the sides slope steeply from the rounded median part. Anterior lobe of middle body subcircular in outline, reaching anterior margin in the midline, anterolaterally curving down to flattened border; near base of small triangular anterior wing this border passes into the gently convex lateral border; lateral border furrow deep just behind anterior wing, becoming shallower posteriorly and running into middle furrow; posterior border a narrow convex band, bearing raised lines, margin gently curved convexly posteriorly; macula a small, slightly raised oval area situated midway along middle furrow; posterior lobe of middle body crescentic in outline, flattened. Margin of borders bent down but not curled under to form a doublure; posterior wing a small rounded projection from this bent-down margin at the posterolateral angle, margin excavated between the wings. The outline and curvature of the transverse median part of the anterior edge of the hypostome is such that it will not fit exactly against the inner edge of the cephalic doublure (compare figs. 6, 9 with figs. 2, 3, Pl. 32). Further, these edges are not thick and sharply transected as are, for example, the edges of the cheek along the dorsal facial suture. This suggests that the anterior edge of the hypostome did not lie against the inner edge of the cephalic doublure along a hypostomal suture. The hypostome may have been attached only by musculature to the dorsal cephalic exoskeleton. If the exoskeleton is reconstructed with the tip of the anterior hypostomal wing lying close to the anterior boss, then the anterior part of the hypostome lay both above and in front of the cephalic doublure, as suggested in Text-figure 8c.

External surface of occipital ring and median lobe of glabella (excluding the muscle areas) and posterior part of the cheek bearing closely and irregularly spaced small pits (Pl. 32, fig. 23); similar pitting may be visible on the middle body of the hypostome. Anastomosing raised lines run longitudinally on the rounded angles of the frontal glabellar spine, the librigenal spine, and the anterolateral edge of the cephalon; similar lines on the outer surface of the inner, ventrally projecting part of the cephalic doublure, and on the lateral and posterior borders of the hypostome. The exoskeleton is thin and differently colored over the hypostomal maculae.

Number of thoracic segments unknown, but presumed in the reconstruction (Text-fig. 8a, b) to be five as in other species of this genus. A few isolated segments have been obtained (Pl. 32, figs. 10, 11, 13-15). Axis about one-third of the width, gently convex, ring flattened and with slight convexity distally; articulating furrow narrow and deep, articulating half ring short (sag.), as is the doublure of the axial ring. Inner part of pleura horizontal, at fulcrum bent down vertically, outer part short, with a narrow doublure rolled closely underneath. Pleural furrow narrow and deep, commencing a short distance out from the axial furrow. Axial and fulcral articulating processes present, a small facet on the anterolateral area of the outer part of the pleura, and a small depression in the posterolateral part of the doublure. These segments are extremely like those of *Ampyx virginiensis* (Pl. 30, figs. 6-13) but may readily be separated by the flatness of the axial ring, narrowness of the articulating and pleural furrows, etc. These segments also match, and fit with, the posterior border of the cephalon and the pygidium of *Lonchodomas carinatus*.

Pygidium (Pl. 32, figs. 18, 19, 21, 22) three times as wide as long, anterior margin straight, transverse, posterolateral margins rounded; gently convex axis tapering and extending back to inner margin of border, inner part of pleural regions horizontal, outer parts bent down to form a steeply sloping border, this border projecting in a gentle convexity behind the axis. Deep articulating furrow and short (sag.) articulating half ring, first axial ring indicated by its slight convexity; behind this ring axis subdivided only by the paired muscle areas; there are two pairs of muscle areas in each ring furrow, a larger outer transversely ovate area, and a smaller inner area, the inner pair being joined across the midline by a narrow band; up to nine ring furrows are indicated by these pairs of muscle areas. Pleural furrows narrow, deep, with a forwardly concave outline; first pleural furrow visible on all specimens, commencing a short distance outside the axis and extending to the inner margin of the border; on some specimens the second, third, and fourth pleural furrow may be seen, each furrow directed outwards and slightly more strongly backwards. Small facet. Outer edge of border thickened, rounded, doublure not extending beneath border; in posterior view the outline of the border having a deep median notch. Axis of pygidium and adjacent part of pleural regions pitted in some specimens, fine, anastomosing raised lines on the outer parts of the thoracic pleurae and the border of the pygidium.

Discussion. Lonchodomas carinatus was described by Cooper (1953, pp. 17-18, pl. 7, figs. 12-17, 19-23), the holotype coming from the present locality 2. Material from the other localities mentioned here appears to be identical with that from locality 2. The cranidium, thorax and pygidium of *L. carinatus* are extremely like those of the type species *L. rostratus* (Whittington, 1950b, pp. 556-557, pl. 74, figs. 11-15, text-fig. 7), which comes from beds in Norway of the same age as the lower Edinburg formation. *L. carinatus* cannot be compared with *L. sublaevis* Raymond (1925, pp. 40-41, pl. 2, figs. 11, 12,) because the type material is too poor for any comparison, nor can it be compared with *L. punctatus* Cooper (1953, p. 18, pl. 4, figs. 20-21) because only the pygidium of this species has been described in detail. The type material of *L. politus* Raymond (1925, pp. 39-40, pl. 2, figs. 8-10), consisting of two cranidia and a pygidium, cannot be distinguished from specimens of the same size in the present material. However, the free cheek of *L. politus* is not known, hence it is uncertain whether or not the librigenal spine had the hooked form characteristic of *L. carinatus*. I hesitate to regard *L. carinatus* as a synonym of *L. politus* without this information. Cranidia and pygidia from Tennessee identified by Cooper (1953, Pl. 6, figs. 1, 2, 5-8, 10) as *L. politus* differ from *L. carinatus* in that the carina is absent on the anterior part of the glabella, there are no pits in the external surface of the fixed cheek, and the pleural regions of the pygidium slope in toward the axial furrows and the distal parts of the external surface exhibit more pleural furrows.

In species of *Lonchodomas* from Scotland and Oklahoma (Whittington, 1950b, p. 557) the librigenal spine is long and gently curved, rather like the corresponding spine in *Ampyx*. Through the kindness of Professor Marshall Kay I have examined material attributed to *Lonchodomas halli* (Billings, 1861) from the Youngman formation, Highgate Springs, Vermont (Kay, 1958, p. 83). Cranidia and pygidia of this Middle Ordovician species are associated with free cheeks bearing a librigenal spine having much the same form as that of *L. carinatus*. An associated hypostome is also like that of the Virginia species. Evidently *L. halli* from Highgate Springs, Vt. (one of Billings' type localities) is a species closely related to *L. carinatus*, and these two species are the only ones so far known with these peculiar hooked librigenal spines. According to Cooper (1956, pp. 31-32, Chart 1) the Youngman is of the same age as the early Edinburg limestone.

Development

One enrolled degree 1 exoskeleton (Pl. 33, figs. 1-4, 7), lacking free cheeks, and isolated cranidia of similar size (Pl. 33, figs. 5, 6, 8) are known. Length of glabella of latter (excluding frontal spine) 0.65 mm.; width of cranidium 1.35 mm. Glabella subdiamond-shaped in outline, moderately convex, with a rounded crest from which the flattened sides slope steeply, occipital ring gently convex, backwardly projecting, occipital furrow shallow medially, represented distally by faint depressions; anterior part of glabella extended into a long, gently upwardly curving frontal glabellar spine, this spine suboval in cross-section; in lateral view two raised longitudinal ridges on the proximal part of the frontal glabellar spine; these ridges unite distally, proximally they run on to the anterior part of the glabella and die out. Fixed cheeks gently convex, triangular in outline, posterior border defined only in the outer part by a shallow posterior border furrow that is deepest just inside the facial suture; in lateral view facial suture only slightly bowed inwards along lateral margin of fixed cheek, anteriorly two branches confluent and bounding anterior margin of glabella. Thoracic segment relatively long (sag. and exs.), convex axial ring and pleural furrow becoming deepest distally; outer part of pleura short (tr.), bent down vertically, fulcrum running in a curve outward and backward so that the anterolateral margin of the segment fits closely beneath the bent-down posterolateral portion of the fixed cheek (Pl. 33, fig. 3). Transitory pygidium three times as wide as long, axis gently convex, divided obscurely into two rings and a wider (tr.) rounded, gently convex, posterior part. Pleural region horizontal beside anterior part of axis, posterolateral and posterior parts curved downwards so that close to, and behind, the axis they slope almost vertically, and in this region there is a shallow median notch in the outline; first pleural furrow shallow, faint interpleural groove, second and third pleural furrows extremely faint; narrow raised rim.

Larger cranidia (original of Pl. 33, figs. 9, 11, 12, of width 1.8 mm., of Pl. 33, figs. 14, 16, 17, of width 2.4 mm.) have been associated with free cheeks of appropriate size. The frontal glabellar spine is now subsquare in cross-section, each side excavated and a ridge running longitudinally along the angle, the spine itself with a reduced upward curvature, almost straight. The surface of the frontal lobe of the glabella below the base of the spine is now flat rather than convex, and where it is bounded by the suture it has assumed the characteristic outline of the holaspis. The free cheek and doublure are thus much like those of larger specimens, except that in the smaller specimen (Pl. 33, fig. 11) that part of the free cheek outside the suture is relatively narrower (tr.), and the librigenal spine is bent, not hooked, so that the proximal portion runs outward and backward, the distal portion slightly inward and backward. In the larger specimen (Pl. 33, fig. 16) the free cheek has approximately the form of the adult, being wider (tr.), and the librigenal spine has assumed the hooked form and subsquare cross-section, though the hook is not quite so acute as in the larger specimens. A transitory pygidium of width 1.65 mm. (Pl. 33, figs. 10, 13, 15) has the axis tapering back, six rings outlined by ring furrows which become progressively fainter posteriorly, and three pleural furrows. The rim is less pronounced than at degree 1 (Pl. 33, fig. 7), the outline posterolaterally smoothly curved; in posterior view the border shows the deep and acute posterior notch. An enrolled exoskeleton of degree 4, lacking the free cheeks (Pl. 33, figs. 19, 22, 23, 26, 29, 30; the second thoracic segment lies edgewise between the first and third, the extremity of the left pleura being visible in the ventral view — Pl. 33, fig. 29) has the cranidium much like that of larger specimens. The four thoracic segments decrease in length (sag. and exs.) posteriorly, and in the last three segments the fulcrum is directed progressively more strongly inward as well as backward. The transitory pygidium is partly concealed in this specimen, but an isolated example of similar size (Pl. 33, figs. 18, 21) has four axial rings and three pairs of pleural furrows visible.

Cephala up to the largest size obtained (Pl. 32, figs. 1, 4, 5, 7, 16, 20) show little further change, the glabella becoming slightly more convex in longitudinal profile, and the lateral concavity in the facial suture slightly more pronounced. Pygidia of larger size (Pl. 33, figs. 20, 25; Pl. 32, figs. 18, 19, 21, 22) likewise show little change, the pleural furrows become decidedly concavely-curved forward, and the median notch in the border slightly shallower.

Genus AMPYXINA Ulrich, 1922

Type Species. Endymionia bellatula Savage, 1917. Redescribed by Whittington, 1950b, p. 557, pl. 73, figs. 7-8. At that time it was not realized that the type specimens were in the U. S. National Museum, numbered 72140. The original of Plate 34, figure 1, an external mould in which the posterior part of the cranidium conceals much of the first thoracic segment, is the holotype.

Discussion. Besides the type and the two species described below, others placed here come from England, Scotland and Sweden (Whittard, 1955, p. 25). Because of the different ways in which these specimens are preserved it is difficult to make comparisons, or to be sure of such features as the convexity and lobation of the glabella, and nature and disposition of the lateral glabellar furrows. The glabella in the type species is rather wider than that of other species, the basal glabellar lobes are represented by shallow oval pits, and the alae merge at the inner posterior corner into the extremity of the occipital ring. In *A. powelli* (Pl. 34, figs. 3-13), *A. wothertonensis* Whittard, 1955 (pl. 3, figs. 1-4), and *A. lanceola* n.sp. (Pl. 35, fig. 32) three pairs of lateral glabellar furrows appear as subcircular shallow pits. The alae in *A. powelli* and *A. lanceola* (Pl. 34, figs. 15, 16) are like those of the type species, whereas in *A. wothertonensis* and *A. aldonensis* (Pl. 28, fig. 13) they appear to be completely cut off from the occipital ring and posterior border by a furrow, perhaps because the latter specimens are internal moulds. In the pygidium the nature of the ribs between the pleural furrows appears to vary — in the type species and *A. wothertonensis* these ridges are broad and flat-topped, whereas in *A. powelli* and *A. lanceola* n.sp. (Pl. 34, figs. 25-27) they are narrow with steeply sloping sides. It is shown here (Pl. 35) that a frontal glabellar spine is present in the development of *Ampyxina.* There is no sign of this spine in the largest specimens of some species, but in *A. lanceola* n.sp. there is a short frontal glabellar spine in the largest specimens, as there is in *A. aldonensis* (Reed, 1935) (this paper, Pl. 28, figs. 11, 13).

Ampyxina powelli (Raymond, 1920)

Plate 34, figures 3-13; Plate 35, figures 1-25.

Raphiophorus powelli Raymond, 1920, pp. 276-277; Raymond, 1925, pp. 32-33, pl. 2, figs. 1, 2.

Ampyxina scarabeus Butts, 1941, p. 75, pl. 82, figs. 1-3; Cooper and Cooper, 1946, pl. 3, figs. 11, 12.

Ampyxina powelli, Cooper, 1953, pp. 13-14, pl. 4, figs. 1-9, 12(?).

Holotype. Museum of Comparative Zoology, no. 1598, from the Edinburg formation, Liberty Hall facies, Catawba Valley, Va.

Figured Material. USNM, from Lower Edinburg limestone, localities 5 and 14.

Description. The new material makes possible the following additions to Cooper's description: —

Occipital ring narrow (sag. and exs.), strongly convex (Pl. 34, figs. 10, 12, 13), in dorsal view curved convexly backward. Occipital furrow deep, curving forward distally and ending against the side of the deep, subcircular, basal glabellar furrow (on the inner surface, Plate 34, figure 6, this lateral glabellar furrow appears as a low, circular, raised area). In front of occipital ring, glabella expands forward to maximum width adjacent to the anterolateral cephalic border, frontal lobe gently rounded; anterior part of glabella moderately convex, that part in front of occipital ring strongly convex, sloping steeply to occipital furrow at basal glabellar furrow. Second and third (from the posterior) lateral glabellar furrows appear as small, suboval, slightly depressed areas over which the exoskeleton is thinner (these thin areas are broken through on right side of original of Plate 34, figure 3); the second situated opposite the anterior end of the ala, the third a short distance behind the anterior pit, both adjacent to the shallow axial furrow. Anterior pit deep (Pl. 34, figs. 6, 10, 13). Frontal lobe of glabella overhangs anterior cephalic border, and is separated from this border by a shallow preglabellar furrow (Pl. 34, fig. 12).

Ala (referred to by Cooper, 1953, p. 13, as basal lateral lobe of glabella) gently convex, of length (sag.) about one third that of glabella (Pl. 34, figs. 3, 4, 6, 12, 13), separated from the glabella by a shallow axial furrow and from the cheek by a broad shallow alar furrow; inner posterior corner of ala merges into the posterior border adjacent to the occipital ring; outer, posterior part of ala separated from posterior border by a shallow posterior border furrow. Cheek (Pl. 34, figs. 7, 8, 10-13) moderately convex, narrow anterolateral border defined by a deep border furrow which dies out, both as it approaches the anterior branch of the suture and the base of the librigenal spine; posterior border furrow curves forward distally so that the posterior border widens, furrow expands into shallow pit just inside facial suture; cheeks united in front of glabella by narrow (sag. and exs.) convex frontal area. Facial suture curves around pit at extremity of posterior border furrow and runs inward and forward across the cheek with a slight sinuosity, the two branches meeting in a smooth curve along the anterior border. Librigenal spine arises from outer and upper surface of cheek at genal angle, is long and tapering, and curves to run directly backward beyond the pygidium. A narrow doublure (Pl. 34, figs. 7, 8), not crossed by median or connective sutures, unites the free cheeks anteriorly; this doublure is horizontal anterolaterally and anteriorly, and a shallow groove runs just inside the smoothly curved inner margin; beneath the base of the librigenal spine the doublure narrows and there is no doublure along the inner part of the posterior border.

Three specimens of a hypostome (Pl. 34, figs. 5, 9) attributed to this species occur with the abundant material at locality 14. Outline subrectangular, slightly wider than long, anterolateral portion projecting slightly laterally; middle body moderately convex, most strongly so anteromedially. Narrow convex border becomes defined at outer part of anterior margin and curves around to follow lateral and posterior margins. An oval, longitudinally elongate, gently convex area situated inside the posterolateral border. Margins of border bent up vertically but not curled under to form a doublure. Small projection from posterolateral part of this margin forms posterior wing. Margin of border between wings excavated in shallow notch.

Thorax (Pl. 34, figs. 3, 4) of five segments, the anterior markedly longer (sag. and exs.) than the succeeding four, which are progressively shorter backward. Axis about one-quarter the width, axial rings narrow (sag.), convex, curved arcuately backward, articulating furrow deep, with deep appendiferal pit situated a short distance inside the axial furrow. Articulating half ring absent on first segment, on succeeding four segments about as long (sag.) as the axial ring. Pleurae extend out horizontally, are flexed down distally, and at the fulcrum a narrow (tr.) portion is bent down vertically and curled under to form an extremely narrow doublure. Pleural furrow of first segment curved convexly forward, on succeeding segments directed transversely, becoming deeper on outward sloping portion. Outer parts of pleurae facetted, facet received by depression in doublure of preceding segment. Pygidium (Pl. 34, figs. 3, 4) with axis reaching back to margin of inner part of pleural regions, border bent down steeply, in posterior view a median notch in the margin. Four to six axial rings outlined by ring furrows which are deepest distally; five pairs of pleural furrows which deepen distally are successively directed more strongly backward and have a distal flexure.

External surface smooth, except for anastomosing raised lines on border of cephalon and outer parts of pleurae of thorax and pygidium.

Development

Smallest known specimens are isolated cranidia (Pl. 35, figs. 1-3), of width (tr.) 0.69 mm. Glabella suboval in outline, moderately convex, the flattened sides sloping from the rounded keel; narrow occipital ring, large deep subcircular basal furrow; frontal lobe prolonged into a thick frontal glabellar spine. Posterior border of convex fixed cheek defined only distally by a pit; ala cannot be distinguished. Next largest specimen is a complete exoskeleton (lacking the hypostome) of degree 2 (Pl. 35, figs. 5, 6, 10, 11). The glabella has a long frontal spine, the alae are well defined by axial and alar furrows, and merge with the innermost part of the posterior border; outside the ala is the posterior border furrow; librigenal spine long and directed backward. First thoracic segment longer than the second and having the characteristic forward curve of the pleural furrow. On the pygidium three axial rings and three pairs of pleural furrows may be distinguished, the pleural furrows straight, lacking the distal backward curve. External surface granulate, a row of short spines along the cephalic doublure, similar spines on the posterior border just inside the base of the librigenal spine.

In exoskeletons of degree 3 (Pl. 35, figs. 4, 7-9) the glabella is sharply keeled, but in exoskeletons of degree 4 (Pl. 35, fig. 12) the keel is less sharp. In small holaspides (Pl. 35, figs. 13, 14) the frontal glabellar spine is about one-quarter the length (sag.) of the remainder of the glabella, the pleural furrows of the pygidium have the characteristic distal backward curve, the external surface is granulate, and there are still short spines on the posterior border just inside the base of the librigenal spine. In the largest holaspides (Pl. 34, figs. 3, 10-13) the frontal glabellar spine may be absent or may be represented by a small tubercle; the external surface appears smooth and there is no trace of the short spines.

Ampyxina lanceola n.sp.

Plate 34, figures 14-28; Plate 35, figures 26-35.

Ampyxina elegans Cooper, 1953 (part), USNM 116443a,b, originals of Cooper's plate 4, figures 10, 11 (reproduced at X8, not X4, as stated by Cooper).

Holotype. USNM 137692 (Pl. 34, figs. 14-17, 22), locality 16.

Other Material. Paratypes USNM 137693a-c; all figured material in U. S. National Museum.

Geological Horizon and Localities. Lower Edinburg limestone, locality 16; Effna limestone, four miles southwest of Bland Court House, Va.

Description. This species occurs quite commonly at locality 16 and may be distinguished from *Ampyxina powelli* by the following characters:

Glabella (compare Pl. 34, figs. 14-17, 22, with Pl. 34, figs. 10, 12, 13) more convex, in dorsal aspect projecting farther in front of the cephalic border, and in the largest specimens bearing a short frontal glabellar spine about one-quarter the length of the rest of the glabella; portion of glabella in front of the occipital ring stands relatively higher and slopes down more steeply to the occipital furrow. Basal lateral glabellar furrow represented by a deep sub-circular pit; in front of this two further furrows (Pl. 35, fig. 32) are faintly discernible as oval areas over which the exoskeleton is thinner, and are situated a short distance up the side of the glabella; the anterior is the smaller. Alar furrow broader and deeper, and the ala is more inflated, separated from the posterior border by the posterior border furrow; this furrow becomes extremely faint behind the inner, posterior corner of the ala, so that here the ala merges into the extremity of the occipital ring. Lateral border of the cheek less strongly curved outside and just in front of the librigenal spine, consequently the free cheek is relatively narrower (tr.) (compare Pl. 34, figs. 14, 15 with Pl. 34, figs. 10, 13). Lateral and anterior cephalic borders narrow, convex, curled under in the narrow doublure which is convex ventrally (Pl. 34, fig. 16). Inner margin of anterior part of doublure faces upward and is rounded, not having the appearance of being a sutural junction. The well preserved specimens show clearly the anterolateral border furrow dying out as it approaches the facial suture (Pl. 34, fig. 17), only an extremely shallow border furrow crosses the anterior part of the fixed cheek, and the preglabellar furrow runs into the axial furrow and separates the glabella from the anterior border.

Pygidium (compare Pl. 34, figs. 25, 27, with Pl. 34, figs. 3, 4) is somewhat more triangular in outline, for the axis and adjacent part of the pleural regions project slightly posteriorly; pleural furrows deeper and broader, especially distally, so that they are separated by narrower, sharper ridges. External surface finely granulate, in some specimens slightly coarser granules on the posterior part of the glabella and a row of tiny spines (Pl. 34, fig. 21) along the posterior margin of the occipital ring and posterior border.

The small cranidia of *A. lanceola* (Pl. 35, figs. 26-29, 32, 35) differ from those of comparable size of *A. powelli* (Pl. 35, figs. 17-24) mainly in the higher glabella and stouter frontal spine. Small pygidia (Pl. 35, figs. 30, 31, 33, 34) differ in outline and in the width of the distal part of the pleural furrows.

Discussion. A cranidium and pygidium placed in *Raymondella elegans* by Cooper (1953, pl. 4, figs. 10, 11) are here placed in *Ampyxina lanceola* n.sp.

The type material of *Ampyxina aldonensis* (Reed, 1935) (Pl. 28, figs. 10, 11, 13) from strata of comparable age in Scotland, shows that this species is extremely similar to *A. lanceola,* particularly in the outline of glabella, the presence of the frontal glabellar spine, the convexity of the alae, and the curvature and width of the pleural furrows of the pygidium.

Genus RAYMONDELLA Reed, 1935

Discussion. The type species, *Raymondella macconochiei* (Nicholson and Etheridge, 1879), has been redescribed (Whittington, 1950b, pp. 558-559, pl. 74, fig. 10; pl. 75, figs. 1, 2), and *R. elegans* Cooper, 1953 is remarkably similar to it. Among raphiophorids *Raymondella* (Pl. 36) seems most closely related to *Ampyxina* (Pls. 34, 35), as comparison between illustrations will show. *Raymondella* differs from *Ampyxina* in form of the glabella (compare Pl. 36, figs. 1-5 with Pl. 34, figs. 1-17, 22) in front of the occipital ring — the basal part is narrow, sloping upwards, and expanding rapidly into a spherical frontal portion which projects and overhangs well in front of the anterior cephalic border; the basal lateral glabellar furrow is a subcircular, deeply impressed pit lying immediately in front of the outer part of the occipital ring; in front of this furrow the glabella expands rapidly. The ala is smaller, subcircular in outline and defined by a deep, broad, alar furrow which runs backward and slightly outward from the axial furrow to the posterior border furrow. The convex cheek of *Raymondella,* inside the border furrows, is crossed by raised anastomosing ridges, a type of sculpture that is not known in *Ampyxina.* Axial rings of thorax and pygidium (compare Pl. 36, figs. 24-26, 29-32, 33, 34, 37, with Pl. 34, figs. 1, 3, 4, 18-20, 25-27) more convex, articulating furrows and appendiferal pits deeper, pleural furrows deeper, and that of the first thoracic segment (Pl. 36, figs. 24-26) lacking the curve convex forward of *Ampyxina* (Pl. 34, figs. 3, 18), pleural furrows of pygidium wider distally and separated by narrow, high ridges.

Raymondella elegans (Cooper, 1953)

Plate 36

Ampyxina elegans Cooper, 1953 (part), p. 14, pl. 4, figs. 14, 15, 16, 18, and 19. The originals of Cooper's figures 10 and 11, plate 4, are here referred to *Ampyxina lanceola* n. sp., and those of his figures 13 and 17, plate 4, to the pygidium of *Tretaspis sagenosus* n. sp.

Holotype. USNM 116445C, a cranidium from the present locality 7.

Figured Material. USNM 116446, original of Cooper, 1953, pl. 4, fig. 16; additional material figured here, in U. S. National Museum.

Geological Horizon and Localities. Lower Edinburg formation, localities 3, 7, 16; Cherry Grove, 4 miles northwest of Linville Station, Rockingham Co., Va.

Description. Largest cranidium here figured (Pl. 36, figs. 1-5) of maximum width 3.25 mm. Occipital ring narrow (sag. and exs.), convex, gently arcuate backward; deep, wide, occipital furrow passes distally into the subcircular pit of the basal lateral glabellar furrow; between these furrows glabella narrow, convex, stalklike, in front of these furrows expanding rapidly into the subspherical median and frontal portions, which project forward and downward over the anterior border; maximum width at about two-fifths the length. Short, blunt, frontal glabellar spine situated on the vertical anterior slope, axial furrow and anterior pit deep.

Alar furrow diverges from the axial furrow at a point about opposite two-thirds the length of the glabella, and runs backward and slightly outward to the posterior border furrow, outer slope steep. Between the alar and axial furrows a triangular area is defined which is depressed below the fixed cheek, and is gently convex only at the inner posterior corner; this convex portion is subcircular in outline and is here termed the ala. The posterior border furrow becomes shallower as it passes inward behind the ala, and thus the inner posterior corner of the ala is separated by only a slight depression from the extremity of the occipital ring. Cheek convex, sloping steeply anterolaterally to the narrow convex border, which is defined by a deep border furrow; border furrow becomes shallow as it approaches the facial suture, narrow convex anterior border separated from the glabella by the deep preglabellar furrow. Two branches of facial suture confluent anteriorly along the margin of the border, laterally having a sinuous course across the cheek. Librigenal spine originates from the posterolateral border and upper posterolateral surface of the cheek, and curves to run directly backward. Cephalic doublure narrow laterally and anteriorly, convex ventrally, absent along posterior border and beneath occipital ring. Hypostome unknown. Posterior border convex, bent down distally, posterior border furrow deep, a distal pit just inside the point where it is crossed by the facial suture.

Only isolated thoracic segments known (Pl. 36, figs. 24-26, 29-32). The anterior segment can be recognized by the curved outline of the anterolateral part of the pleura where it fits beneath the posterior cephalic border. Other segments have a rectangular outline to the distal part of the pleura. Axial ring narrow (sag. and exs.) and convex, articulating furrow deep, appendiferal pit deep and elongate, situated a short distance in from the axial furrow, appendifer a thick triangular projection. Pleural furrow deep and broad, running out transversely, flanked by convex ridges. Outer part of pleura bent down gently, the outermost part flexed vertically and curled under to form a narrow doublure. Anterolateral angle of pleura facetted, and doublure with a depression to receive the facet of the following segment during enrollment. Pygidium (Pl. 36, figs. 33, 34, 37) four times as wide as long (sag.), convex axis divided by deep furrows into four rings. Inner part of pleural region horizontal, deeply excavated by three pleural furrows that widen rapidly distally, these furrows separated by strong interpleural ridges which run outward and backward to join the rim. Border bent down almost vertically, outline of outer edge in posterior view sinuous, with a median notch. Doublure extremely narrow.

External surface of glabella, axial rings, and ridges of thorax and pygidium granulate, the granules coarsest in a row along the occipital and axial rings, the posterior cephalic border, and the posterior ridge of the thoracic pleurae. Cheek inside border furrows crossed by raised, anastomosing lines which run subparallel to the anterolateral margin. On the cephalic doublure, the outer parts of the pleurae, and on the border of the pygidium, raised lines run subparallel to the margin.

Discussion. The pygidium attributed to *Raymondella elegans* by Cooper (1953, p. 14, pl. 4, figs. 13, 17) is considered here to be that of *Tretaspis sagenosus* n.sp. These two species occur together at localities 3, 7, and 16, *Tretaspis sagenosus* occurring rarely at a few other localities. The associations of exoskeletal parts made here are based on morphological comparisons between occipital ring and posterior border of cephalon, and thoracic segments and pygidia. They seem to be upheld by the likeness between the pygidium of *R. elegans* and the type species, and the likeness between the pygidium of *Tretaspis sagenosus* n.sp. and that of other species of this genus.

Cooper (1953, p. 14) states that the width of the holotype cranidium is 4.8 mm. This figure may have been printed in error, since, using the magnifications given in his plate 4, figures 14, 15, 18 and 19, the width of the holotype cranidium appears to be about 3.5 mm. The largest specimens I have seen in both Cooper's and my material are of about this size.

Another species of *Raymondella,* from the Oranda formation, Chambersburg, Pa., is that described by Cooper (1953, pp. 14-15) as "*Ampyxina* sp." The cranidium is typical, but the glabella (Pl. 28, figs. 15, 16, 19) appears to differ from that of *R. elegans* in having flattened sides and a rounded median keel.

Development

A size series of cranidia from a width of about 1.0 mm. to 3.5 mm. is known. The smallest cranidia (Pl. 36, figs. 18, 19, 22,

23) are like those of comparable size of other raphiophorids (Pl. 31, figs. 7-9; Pl. 35, figs. 5, 6, 10, 11), the glabella clavate, pinched in in front of the occipital ring by the basal glabellar furrows, frontal lobe projecting beyond the anterior border and continued by a thick, straight, frontal glabellar spine. A relatively large triangular area is enclosed between the alar and axial furrows, and the posterior border furrow is shallow. As size increases (Pl. 36, figs. 16, 17, 21; 10, 15, 20; 12-14; 8, 9; 6, 7, 11), the most conspicuous changes occur in the glabella. In the early stages the glabella is keeled, with flat, steeply sloping sides. As the part in front of the basal glabellar furrows swells up to become subspherical, the median portion becomes higher and rounded in transverse section, the transverse profile changing from triangular to circular; the frontal part of the glabella bulges forward and downward over the anterior border, and the frontal glabellar spine is progressively reduced to the short, blunt-tipped spine of the largest cranidia. The posterior border furrow becomes deeper with increasing size, and at all times it seems to separate the inner posterior convex portion of the ala from the posterior border.

The smallest known pygidia (Pl. 36, figs. 27, 28) differ from the largest in not exhibiting the fourth axial ring.

External surface of cephalon in the small stages granulate, row of tiny spines around the anterior and lateral margin. In the larger specimens the surface is similar, except that on the cheek granulation has fused to form the anastomosing lines.

Family ENDYMIONIIDAE Raymond, 1920

Genus SALTERIA Thomson, 1864

SALTERIA AMERICANA Cooper, 1953

Plate 28, figures 9, 12, 14, 17, 18

Discussion. Cooper (1953, pp. 12-13, pl. 3, figs. 8-10) based this species on material from the lower part of the Liberty Hall facies of the Edinburg limestone in Rockingham and Pulaski counties, Va. A few additional silicified specimens have been obtained from the present locality 14.

Occipital ring is extremely narrow (sag. and exs.); the "raised posterior carina" is not evident. In front of the preglabellar furrow is a narrow (sag. and exs.) preglabellar field, separated by a shallow anterior border furrow from the narrow anterior border. No trace of genal caeca. Cranidium bounded by facial suture which runs forward in a curve convex outward across the posterior border, and then forward and slightly inward across the cheek in a sinuous course, reaching the anterior border outside the projected line of the axial furrow and running along the margin of this border. Free cheek and cephalic doublure unknown.

Thorax of 7 segments, the anterior segment the longest (sag. and exs.). Pleurae inflated, inner part horizontal, crossed by a deep, narrow, pleural furrow which runs in a curve concave forward and deepens distally. Distal part of pleurae bent down in two stages, the first sloping gently outward, the outermost part, beyond the end of the pleural furrow, narrow (tr.) and bent down vertically. Pygidium more than twice as wide as long (sag.). Pleural regions with a broad, shallow, border furrow outside which is a convex border, the outermost part of this border narrow and sloping almost vertically. Six pairs of deep, narrow pleural furrows running in curve concave forwards, dying out at the inner margin of the border furrow. Doublure of thoracic pleurae and pleural regions extremely narrow, being merely the tightly rolled-under edge of the exoskeleton. Sculpture of the external surface of the exoskeleton not well preserved, but fine raised lines run along the doublure of the pygidium.

As Cooper (1953, p. 13) pointed out, this species is exceedingly like the type species *Salteria primaeva*, from the Balclatchie beds, lower Middle Ordovician, Scotland (Reed, 1903, pp. 43-44, pl. 4, figs. 13, 14). I have placed this genus in the family Endymioniidae, but the cephalon of *Salteria* resembles that of *Seleneceme* (Whittington, 1952a, p. 4, pl. 2, fig. 13) in the subcircular outline of the glabella, narrowness (sag.) of the occipital ring, breadth of the posterior cephalic border, and course of the facial suture.

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