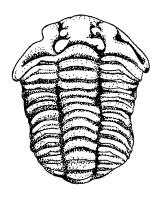
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TRILOBITES OF THE HENRYHOUSE FORMATION (SILURIAN) IN OKLAHOMA



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TRILOBITES OF THE HENRYHOUSE FORMATION (SILURIAN) IN OKLAHOMA

K. S. W. CAMPBELL*

ABSTRACT

A small fauna of trilobites from the Henryhouse Formation of Oklahoma consists of eleven species referred to ten genera. Among the genera, the cheirurid Anasobella (type species A. asper, new species) and the phacopid Ananaspis (type species Phacops fecundus communis Barrande) are new. Ten of the species are new. The fauna is peculiar in that it lacks illaenids and lichids.

Certain representatives of the subfamilies Phacopinae and Phacopidellinae are discussed, and Phacops Emmrich, Reedops Richter and Richter, and Eophacops Delo are redefined. Eophacops is transferred from the Phacopinae to the Phacopidellinae, and Phacops musheni Salter and P. trapeziceps Barrande are referred to it rather than to Phacopidella. A new genus, Acernaspis, with type species Phacops orestes Billings, is erected. A suggested phylogeny for the Silurian to Middle Devonian phacopinids and phacopidellinids is outlined.

The Henryhouse material is well preserved, and morphological detail is available for almost all species. Attention is drawn to the systematic value of fine surface structures.

The age of the fauna, as indicated by the trilobites, is late Wenlockian to early Ludlovian. Elements of the faunas of Bohemia, Great Britain, and northeastern United States are recognized. It is noteworthy that the fauna lacks the strong Bohemian affinities of the one of similar age from the Gazelle Formation of California.

INTRODUCTION

This study of the trilobites of the Henryhouse Formation is based almost entirely upon the collections of others. The bulk of the material was assembled by the Oklahoma Geological Survey and The University of Oklahoma, and is now housed in the latter institution. Other important collections are in the U. S. National Museum, Washington, D. C., and the Peabody Museum, Yale University.

In all, approximately 500 specimens have been examined. About two thirds of this number belongs to the species Calymene clavicula, new species, most specimens of which are well preserved and commonly occur as articulated skeletons. Dalmanites rutellum, new species, and Ananaspis guttulus, new genus and species, are the next most abundant, with sixty-five and thirty-eight specimens, respectively. Of the remaining species, each is represented by between four and twenty specimens, except for Anasobella asper, new genus and species, which is represented by two specimens, and Leonaspis sp., which has only one. Adequate material is available for the description of all species save Kosovopeltis nebula, new species, and

K. bypha, new species, which lack free cheeks and cephalon, respectively; Dudleyaspis desolator, new species, for which no thorax or pygidium is available; and Leonaspis sp., known only from a free cheek. The preservation is good. The exoskeleton is almost invariably present and shows fine detail. With the use of needles, brushes, and an airblasting machine it has been possible to remove the relatively soft marly matrix from the specimens without excessive damage to the surfaces. It has also been possible to free the rostral plates and hypostomes of certain species for close study.

The work was undertaken as part of a program to investigate and describe the faunas of the Hunton Group, initiated and sustained by T. W. Amsden, who has studied the stratigraphy and sedimentation of the group (Amsden, 1956, 1957, 1960, 1962) and described the brachiopods in a series of monographs, alone and with W. P. S. Ventress (Amsden, 1951, 1958a, 1958b, 1963; Amsden and Ventress, 1963). The Henryhouse crinoids have been described by Strimple (1963), the ostracodes and corals by Lundin (1965) and Sutherland (1965), respectively.

The following people, to whom I extend my thanks, have assisted by allowing me access to, or

^{*}The Australian National University, Canberra.

6 DISTRIBUTION

lending me, specimens in their charge: G. A. Cooper, Smithsonian Institution; K. M. Waagé, C. MacClintock, and Mrs. M. Dasch, Yale Peabody Museum; D. J. McLaren and T. E. Bolton, Geological Survey of Canada; Katherine Nelson, University of Wisconsin at Milwaukee; E. Richardson, Chicago Natural History Museum; W. B. N. Berry, University of California, Berkeley; G. Henningsmoen, Palaeontological Museum, Oslo; J. Ernhold Hede, Lund University; Sir James Stubblefield, H. M. Geological Survey, London; H. O. Fletcher, Australian Museum, Sydney; and T. Nicholas, Bureau of Mineral Resources, Australia. Miss J. Shepherd prepared the text-figures. Mrs. M. Korringa assisted with the photography and making the plates. A. J. Boucot and W. B. N. Berry permitted me to use their unpublished correlation chart of the Silurian formations of North America and D. Bruton sent me data on Dudleyasbis. P. K. Sutherland discussed various problems with me and provided some of the specimens. I have enjoyed discussions on points of interpretation and presentation with Leif Størmer and R. P. Tripp. I am particularly indebted to T. W. Amsden for arranging for specimens to be sent to me, for showing me the Henryhouse Formation in the field, and for information on the localities from which various collections have come. And finally it is a pleasure to acknowledge the assistance of H. B. Whittington, who made possible my visit to Harvard University, introduced me to the problem, made available the collections of the Museum of Comparative Zoology and his own collection of literature, and gave advice on all aspects of the work.

The project was undertaken while I was on sabbatical leave from the Australian National University. An Australian-American Educational Foundation award defrayed travel costs, and my stay at Harvard at the Museum of Comparative Zoology was supported by National Science Foundation grant GB3577 to Prof. Whittington. To these organizations I wish to express my thanks.

DISTRIBUTION OF TRILOBITES IN THE FORMATION

Much of the material is not well enough localized to enable determination of its position within the formation. However, I have examined all the trilobites from Amsden's measured sections (table 2; Amsden, 1960); Amsden has localized one of the more important collections made by A. Allen Graffham, and I have small collections from some localities, the positions of which are known precisely.

The most satisfactory data on ranges within the formation come from the Lawrence uplift. In other areas the section is thinner or the fossils are much less common. Considering only the Lawrence uplift and working on a Henryhouse section of 240 feet, the distribution chart is as shown in table 1. The ranges shown are minimal, based as they are upon accurately localized material from a limited area only. Calymene clavicula, Ananaspis guttulus, Fragiscutum glebalis, Cheirurus infensus, and Dalmanites rutellum range through most of the formation and are the more common species in the collection. Among the less common species, Dudleyas pis desolator is equally long ranging, Kosovopeltis nebula and K. hypha are known only from the upper third, Proetus foculus from near the base and the top, and Anasobella asper (two specimens) over an indefinite range in the middle, and possibly lower, part of the formation.

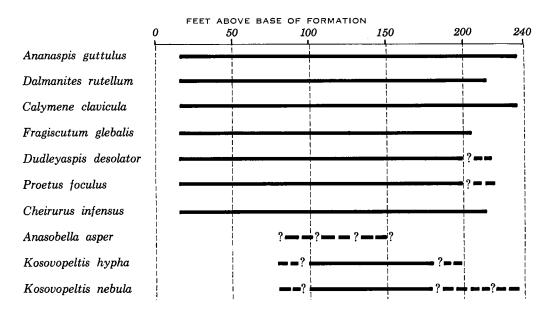
The range indicated for the species of Kosovo-peltis may be too limited because of collecting difficulties. Many of the specimens are from the collections made by A. Allen Graffham in quarrying operations. The exoskeleton of these species is thin, and the pygidium is rather flat and would not be preserved so well as would those of the more convex forms. Broken fragments are not easily recognized and would be overlooked in surface collections.

The evidence of the trilobites therefore tends to confirm the view arrived at from the study of the brachiopods (Amsden, 1951, 1958b) and ostracodes (Lundin, 1965), that the Henryhouse fauna is essentially uniform. For details of the sections listed in table 2, see Amsden (1960, p. 178-286).

As has been noted previously (Lundin, 1965), some of the older collections have not been accurately localized. In connection with this present work it should be noted that the U. S. National Museum specimens said to be from C sec. 4, T. 2 N., R. 6 E., Pontotoc County, are not from the geometrical center of the section, but rather from the NE quarter of the SW quarter.

In addition to the material from Amsden's measured sections and collection localities, a large and important collection was made by Graffham from

Table 1.—Stratigraphic Ranges of Trilobite Species in the Henryhouse Formation, Lawrence Uplift, Oklahoma



what he called the *Calymene* quarry. This locality is now inundated by a small lake. Stratigraphically it was about 80 feet from the upper boundary of the Henryhouse, and geographically it was near C SW 1/4 sec. 4, T. 2 N., R. 6 E., Pontotoc County. The material from this quarry includes several hundred specimens of *Calymene clavicula*, and fewer of

Kosovopeltis nebula Kosovopeltis hypha

Dalmanites rutellum Cheirurus infensus

A small collection was made by Amsden and the author in the upper 30 to 40 feet of the Henryhouse Formation on the south side of Cedar Hill (near section P3), Pontotoc County. This collection contained

Calymene clavicula
Dalmanites rutellum
Cheirurus infensus

RELATIONS WITH FAUNAS ABOVE AND BELOW

The trilobite fauna of the overlying Haragan Formation is known in part. Species described or recorded from it are "Phacops" deckeri Delo, "P." hudsonicus Hall, "P." logani Hall, "P." raymondi Delo, Dalmanites huntonensis Ulrich and Delo, D. linguifer Ulrich and Delo, D. oklahomae Richardson, D. taffi Ulrich and Delo, Neoprobolium sp., Odontochile acuminatus Ulrich and Delo, Cordania falcata Whittington, Leonaspis williamsi Whittington, Dicranurus hamatus (Hall), Miraspis sp. ind., and "Proetus" protuberans Hall (Amsden, 1956; Whittington, 1956b, 1960). In addition to these species, a few undescribed species are in the collections of The University of Okla-

homa. None of the Henryhouse trilobite species has been found in the Haragan, and vice versa. The distinctness of the two faunas is even more marked at the generic level, as can been seen from table 3 (p. 10). The only two genera common to both formations are *Dalmanites* and *Leonas pis*. None of the genera, which elsewhere are limited to Devonian strata, occurs in the Henryhouse, and none restricted to Silurian and older strata occurs in the Haragan.

The underlying Clarita Formation has a rich trilobite fauna also, but to date no species has been described, and, so far as I am aware, none has been listed.

COLLECTIONS

8

Table 2.—Species Collected from the Henryhouse Formation at Localities* of T. W. Amsden (1960)

THICKNESS OF FORMATION (FEET)	INTERVAL ABOVE BASE OF FORMATION (FEET)	UNIT	SPECIES
		tion Cal	- .
	$(SE_{4}^{1/4} sec. 30)$, T. 2 S., R. 1	E.)
183	82-108	Q	Calymene clavicula Ananaspis guttulus Fragiscutum glebalis
	112-124	S	Ananaspis guttulus
	148-183	U	Dalmanites rutellum
	Sact	ion Ca8	
	(NW 1/4 NE 1/4 sec		. 2 W.)
167	127-167	J	Proetus foculus
	Sect	ion Ca9	
(SW 1/4 SW 1/4	/4 sec. 36 and SE 1/4	SE 1/4 sec. 35	, T. 1 S., R. 2 W.)
245	114-150	E	Ananaspis guttulus
	Secr	tion M1	
	(NW 1/4 NW 1/4 se	c. 2, T. 2 S., I	R. 2 E.)
62	30- 46	D	Calymene clavicula Ananasþis guttulus Fragiscutum glebalis Proetus foculus
	46- 56	E	Calymene clavicula Ananaspis guttulus Fragiscutum glebalis Cheirurus infensus
	56- 62	F	Calymene clavicula
	Saat	tion M8	
	(SE 1/4 NE 1/4 sec.		. 2 E.)
70	32- 52	Н	Calymene clavicula Fragiscutum glebalis
	52- 70	I,J	Ananaspis guttulus Dalmanites rutellum Fragiscutum glebalis
	Secti	on M10	
	(SW 1/4 SE 1/4 sec.	33, T. 1 S., R.	3 E.)
28	6- 22	G	Calymene clavicula Ananaspis guttulus Dalmanites rutellum Proetus foculus
	Secti (NE 1/4 NW 1/4 sec.	on M17	2 F)
0.5			•
85	74- 85	Н	Leonaspis sp.

т.	a	R٢	E	2	(cont	1

	TABLE	2 (cont.)	
THICKNESS OF FORMATION (FEET)	INTERVAL ABOVE BASE OF FORMATION (FEET)	TINU	SPECIES
	_	ion M18	
	(SW 1/4 SE 1/4 sec.	17, T. 2 S., R.	1 W.)
191	116-156	I	Fragiscutum glebalis Cheirurus infensus
	Sec	tion P1	
(9	SE_{4} sec. 5 and SW_{5}	•	., R. 6 E.)
247	43- 57	I	Calymene clavicula
	57- 72	J	Fragiscutum glebalis
	72- 74	K	Calymene clavicula
	91-117	M	Ananaspis guttulus
	117-137	N	Calymene clavicula
	153-176	P	Calymene clavicula
	195-203	R	Calymene clavicula Cheirurus infensus Fragiscutum glebalis
	203-223	S	Calymene clavicula Ananaspis guttulus (in situ?)
	Sac	tion P3	
(1)	NE 1/4 sec. 9 and SE 1/		V., R. 6 E.)
233	155-168	P	Calymene clavicula
2,7,7	1//-100	^	Ananaspis guttulus Fragiscutum glebalis
	187-204	S	Dalmanites rutellum
	Sec	tion P4	
			(F)
to	(SW 1/4 SW 1/4 sec. p 15 to 20 feet	3, 1. 2 N., R A	6 E.) Calymene clavicula Ananaspis guttulus
	Collectio	n Locality P5	
	(NW 1/4 NW 1/4 sec	•	R. 6 E.)
	40	,	Calymene clavicula Dalmanites rutellum
	Callantia	n Locality P6	
	(SE ½ SW ½ sec.		6 E.)
	15- 27	. 1, 1. 2 11, 1	Calymene clavicula Ananaspsis guttulus Cheirurus infensus Fragiscutum glebalis Proetus foculus Dudleyaspis desolator
		_	javp.v siavo.
		tion P8	
	(SW 1/4 NW 1/4 sec	. 11, 1. 2 N., I	
		Δ	Calymene clavicula

^{*} Locality-number prefixes indicate counties as follows: Ca, Carter; M, Murray; P, Pontotoc.

Calymene clavicula

Table 3.—Stratigraphic Ranges of Genera and Their Occurrence in the Henryhouse and Haragan Formations

GENUS	TIME RANGE	HENRYHOUSE FORMATION	HARAGAN FORMATION
Ananaspis	Early Silurian-Late Silurian	X	
Ananaspis?, n. gen.	Early Devonian		X
Dalmanites	Silurian-Devonian	X	X
Neoprobolium	Early Devonian		X
Odontochile	Late Silurian-Middle Devonian		X
Calymene	Early Silurian-Middle Devonian	X	
Fragiscutum	Middle Silurian?-Late Silurian	X	
Dudleyaspis	Middle Silurian	X	
Leonas pis	Early Silurian-Middle Devonian	X	X
Miraspis	Early Ordovician-Early Devonia	ın	X
Dicranurus	Early Devonian-Middle Devonia	n	X
Proetus (Proetus)	Ordovician-Middle Devonian	X	
Proetid (undet.)			х
Cheirurus	Late Ordovician-Late Silurian	X	
Anasobella	Middle Silurian?-Late Silurian	X	
Kosovopeltis	Middle Silurian?-Early Devonian	ı* X	

^{*} In Czechoslovakia the genus occurs from the Kopanina to the Lochkov beds. I accept the suggestions of Jaeger (1962) and Solle (1963) that these units span the interval from the base of the Ludlovian to approximately the middle Siegenian.

CORRELATION AND AGE

Correlation within North America.—Amsdem (1951) found a close relation between the brachiopods of the Henryhouse and those of the Brownsport Formation of Tennessee. Trilobites are rare in the Brownsport, the only identifiable material available to me consisting of two species of dalmanitids and two of calymenids. Of these, Calymene clavicula, new species, is the only one also found in the Henryhouse Formation. The dalmanitids apparently belong to undescribed species.

At the species level there are few similarities with faunas from the Great Lakes region, although representatives of Dalmanites, Calymene, Proetus, Cheirurus, and Kosovopeltis are known from the Wenlockian or lower Ludlovian Racine Dolomite. The Ludlovian West Point Formation in Gaspé has a similar species of Cheirurus, C. tarquinius, and forms described as Goldius pompilius (Billings) by Northrup (1939) belong to Kosovopeltis.

It is of interest to note the dissimilarity of the Henryhouse fauna to that of the approximately temporally equivalent Gazelle Formation of California (Churkin, 1961).

Correlation overseas.—In using Silurian trilobites for overseas correlation one is limited by two main factors—the general neglect of the group by paleontologists for the last sixty years and the in-

complete sequence of trilobites in the type Silurian in Great Britain. Perhaps the most complete trilobite succession is in Gotland. The last monographic treatment of these faunas was that of Lindström (1885), and since that date only occasional species have been described. In Dalarne and Estonia the upper half of the Silurian is not represented, but what is available is well known from the work of Schmidt (1881-1907), Warburg (1925) and Öpik (1937), among others. Czechoslovakian trilobite faunas are abundant in the Wenlockian and Ludlovian, and they have been monographed by Barrande (1846, 1852), Prantl and Přibyl (1948, 1949), Přibyl (1946, 1960), Šnajdr (1960), and others. These works are among the most valuable, for they provide clear descriptions and they are well illustrated, but their use is limited by their provinciality. For example, three of the ten Henryhouse genera described herein are unknown from Czechoslovakia, and three of the remainder are the cosmopolitan Proetus, Calymene, and Dalmanites. British descriptive work on Silurian trilobites since Salter's monograph of 1864-1883 is limited to Whittard's (1938) study of the Llandoverian forms from Shropshire, Reed's work (1903-1935) on the Llandoverian at Girvan, and a few isolated descriptions. Further, the best preserved and most adequately illustrated and quoted material is from the Wenlockian, particularly that at Dudley, and this fact produces an imbalance in that these faunas tend to dominate comparative work. This defect is further emphasized by the completely inadequate data available on Ludlovian trilobites (e.g., the summary of the faunas in the Ludlow area by Holland, Lawson, and Walmsley, 1963).

The Silurian trilobite faunas of Russia are becoming known through the work of Weber (1951), Maksimova (1955, 1960, 1962), Chernysheva (1951), and Balashova (1960). However, to date few species pertinent to the present study have been described.

Elsewhere extensive trilobite faunas are known only from Australia, but the bulk of these are known from inadequately illustrated works (Etheridge and Mitchell, 1895-1917), and accurate comparison is not possible. Other works cover only a few species.

The following genera together offer information on the age of the fauna. Kosovopeltis first appears overseas in the early Ludlovian and possibly persists into the Siegenian. K. nebula, new species, most closely resembles K. svobodai Šnajdr from the lower Ludlovian Kopanina beds of Czechoslovakia.

Ananaspis ranges from the late Llandoverian through the Ludlovian. A. guttulus, new species, is closest to A. stokesi (Milne-Edwards) from the upper Wenlockian of Great Britain.

As here defined, *Dudleyaspis* is known overseas only from the upper Wenlockian of England. Nothing is to be gained stratigraphically from specific comparison.

The nearest relative of Calymene clavicula, new species, is C. lata Shirley from the upper Wenlockian-lower Ludlovian of England, and Dal-

manites myops (König) of the same age is closest to D. rutellum, new species.

An attempt is made here and by Whittington and Campbell (1967) to identify a species group centered on *P. concinnus* within the genus *Proetus*. This group occurs only in the Late Silurian. In any case, *Proetus foculus* is not far removed from the type species *P. concinnus* (Dalman) from the Mulde beds (upper Wenlockian) of Gotland. In the overlying Klinteberg beds (lower Ludlovian) it is replaced by *P. conspersus*, a very different species, but *P. morinensis* Přibyl, which is of the *P. concinnus* type, occurs in the Ludlovian of Czechoslovakia.

In summary then, an overseas correlation within the upper Wenlockian-lower Ludlovian is indicated by the occurrence of *Kosovopeltis* and *Dudleyaspis* together. Species comparisons may be thought to favor a late Wenlockian age slightly. However, against this must be set the tendency to overemphasize the late Wenlockian affinities alluded to above.

When correlation with North American formations that can be dated by other fossils is taken into account, no more precise age can be obtained. The trilobite evidence, therefore, is in accord with that of the brachiopods and ostracodes in indicating a position near the Wenlockian-Ludlovian boundary. At present it is not possible to give as definite a determination as can be done with the graptolites (Decker, 1935), which suggests an early Ludlovian age (zone of Monograptus nilssoni).

Repositories.—Specimen-number prefixes indicate repositories as follows: GSC, Geological Survey of Canada; MCZ, Museum of Comparative Zoology, Harvard University; OU, The University of Oklahoma; USNM, U. S. National Museum; YPM, Peabody Museum, Yale University; CNHM, Chicago Natural History Museum.

SYSTEMATIC DESCRIPTIONS

Family SCUTELLUIDAE* Richter and Richter, 1955

Genus Kosovopeltis Šnajdr, 1960

Type species.—Kosovopeltis svobodai Šnajdr, from the Kopanina beds (Ludlovian) of Czechoslovakia.

Remarks.—Two new species are here assigned to Kosovopeltis. One, K. nebula, is known from the cranidium, thorax, and pygidium, and the other, K. hypha, from thorax and pygidium only. Šnajdr (1960, p. 247), in erecting the genus, placed great weight on details of the cephalon and pygidium, and little on the thorax. Consequently, although K. nebula can be assigned with confidence, K. hypha can not.

Attention is drawn to two points in Šnajdr's diagnosis. The median unpaired rib of the pygidium is said to be nonbifurcate, and the width of the pygidial doublure to be about half the length of the postrhachial area. It is noted, however, that the specimens of K. svobodai figured by Šnajdr on his plate 3 (figs. 25, 26) have at least a partial bifurcation of the median pleura, and hence the diagnosis should be modified; and the width of the doublure ranges from 0.6 of the postrhachial area in figured specimens of K. svobodai to 0.42 of the postrhachial area in figured specimens of K. partschi partschi.

One of our species has a bifurcate posterior rib and the other does not. K. hypha has a doublure ca. one-half the length of the postrhachial area, and K. nebula ca. three-quarters. In all other characters, however, K. nebula falls within the range of Kosovopeltis, and I suggest that the diagnosis should be emended to include it.

Range.—Kosovo peltis occurs in the Ludlovian-Gedinnian of Czechoslovakia, in the Ludlovian (?) of the Urals (Šnajdr, 1960), in the Ludlovian of Oklahoma, and in the Wenlockian (?)-lower Ludlovian of Wisconsin.

Kosovopeltis nebula, new species

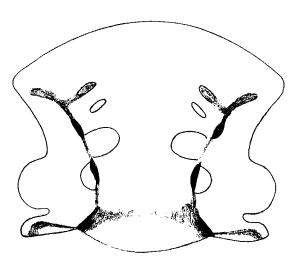
P1. 2, figs. 1-8; p1. 3, figs. 1, 2, 4; text-fig. 1

Types.—Holotype OU 4963A, B and paratypes OU 4963C-E, from SW 1/4 SE 1/4 sec. 4, T. 2 N.,

R. 6 E., Pontotoc County; paratypes OU 5794A, B and OU 5620, from C SW 1/4 sec. 4, T. 2 N., R. 6 E., Pontotoc County.

Other material.—Specimen OU 5621, labeled Lawrence uplift near Ada, but clearly Henryhouse Formation upon the basis of the associated fauna on the same slab.

Description.—Cephalon known from cranidium only; glabella widest at the front, narrowest at the occipital furrow and widening to the posterior margin; ratios of widths at these three positions, 7:3:4; gently curved in both anterior and lateral profiles, and no tubercles present either on the central part or on the occipital ring; axial furrows steep near the posterior border, very shallow at the occipital furrow, deepening slightly anteriorly with slight elongate depressions in the posterior of glabellar furrows 1p, 2p, and 3p; in front of 3p axial furrow becomes very ill-defined; no preglabellar furrow, the glabella curving evenly over to the rostral suture; furrow 1p represented by a slight indentation of the glabella, 2p without a true furrow, but 3p with a distinct but shallow furrow directed inward and slightly forward from the axial furrow approximately a quarter of the distance across the glabella; region of occipital furrow poorly preserved, but furrow very faint. Muscle impressions marked by smooth shell sur-



Text-figure 1. Reconstruction of the cranidium, x4.25, of Kosovopeltis nebula, new species, showing the probable arrangement of the furrows and areas of muscle attachment. Shape of occipital furrow largely conjectural. Terrace lines omitted.

^{*} I.C.Z.N. decision pending.

face, but not all are clearly preserved; 3p is within furrow 3p; 2p is ellipical in outline and is slightly forward of the 2p pit in the axial furrow; 1p is large and apparently almost semicircular, but not clear; lateral muscle scar semicircular and with the edge of pit 1p as its diameter; occipital muscle scars partly obliterated, but apparently rather small. Palpebral lobe gently convex in anterior profile, with a semicircular end in plan, but with the anterior edge wider (tr.) than the posterior; a line joining the outermost tips of the palpebral lobes passes through the rear edge of the lateral muscle scars; facial suture with α close to the edge of the glabella, α - γ straight to very gently convex adaxially, ϵ - ω strongly curved near ω ; ω directly behind δ ; terrace lines generally transverse on the whole cranidium, but tend to parallel the anterior margin near the front of the glabella, and are diverted anterolaterally on the front of the fixed cheeks; no areas enclosed by complete terrace lines.

Pygidium (exclusive of articulating half ring) with length three-quarters of width; anterior edge lateral to fulcral points curving gently around to the lateral margins; posterior outline uniformly rounded; axis (excluding half ring) ca. one-fifth of the total length; axial furrows lightly impressed, becoming weaker posteriorly; a weak and incomplete anterior axial ring formed by shallow furrows uniting on each side with the anterior furrow about one-third of the distance across the axis; shallow longitudinal furrows also present, strongest posteriorly, fading away before reaching the anterior furrow, and separating off the median third of the axis; articulating half ring about one-quarter the length of the remainder of the axis, and with the even curve of its anterior edge broken by a slight median forward bowing; anterior furrow with gentle posterior and an abrupt anterior slope; seven lateral pleurae on either side and a median undivided pleura; the anterior pleurae tend to have gentle anterior and sharper posterior slopes, but more posterior ones progressively more symmetrical; pleural furrows narrow and tend to fade away within about 1 mm of the axial furrow, and 2 mm of the border; deepest within a line joining the fulcra and running parallel to the axial furrow (i. e., on the most convex part of the test); most anterior furrow straight to faintly convex forward, the second straight to slightly concave, and all subsequent ones distinctly concave; inner end of second furrow opposite the faint axial ring, and the most posterior furrows originate lateral to the longitudinal axial furrows; width of posterior undivided pleura at margin between one-seventh and one-eighth of total width; measured along first pleural furrow, the doublure three-fifths the distance from the margin to the axial furrow, and along the posterior pleura the figure is three-quarters.

Ornament pattern distinctive; axis with long terrace lines arranged in a tripartite pattern corresponding with the three longitudinal lobes, weakly convex forward near the front, much more strongly so near the rear; lines tending to fade out in the longitudinal furrows; anterior axial ring sharply marked off by terrace lines directed forward and inward; posterior half of articulating half ring with transverse terrace lines, anterior half smooth; only occasional lines encroach onto the axial furrows, and few cross the pleural furrows; in general, individual lines on the pleurae persistent, in line on opposite sides of pleural furrows, and gently concave anteriorly; this over-all pattern modified at anterolateral corners where lines curve around and become convex forward, and then deflect backward abruptly at the margins to form a neat selvage; in general, direction of the lines on inner part of anterior pleurae 15° to 20° to the straight anterior edge; 7 or 8 lines per mm on middle of median pleura but reduced to 5 or 6 per mm near the margins (all measurements being taken normal to the direction of the lines); on approximately the inner third of doublure, terrace lines widely spaced (ca. 4 per mm) and more strongly curved than inner edge of doublure; on outer two-thirds, lines more closely spaced (8 or 9 per mm near the posterior and 6 to 8 near the anterior) and with a lesser curvature than those farther in, resulting in an irregular zone of discordance around the whole pygidium.

Remarks.—A small, crushed, teratological individual (OU 5621), which has the pygidial ornament of this species (pl. 2, figs. 5, 6), is important because it has a well-preserved thorax. A small fragment of the cranidium is also attached, and it is similar to the one described above. I think it reasonable, therefore, to consider this thorax as representative of the species. The convexity of the rings cannot be determined because of crushing. All rings, except the first, are slightly shorter in the middle (sag.) than at the extremities, and this is correlated with the slight medial expansion of the articulating furrow. The anterior ring is only a third as long medially as laterally, due to a crescentic expansion of the articulating furrow. The pleurae are parallel-edged from the axis to the fulcra, and beyond the fulcra are slightly expanded (exsag.) and gently recurved. Ornament on the rings consists mainly of simple arcuate terrace lines, except for the median posterior portion where the lines are almost directly transverse. On the inner parts of the pleurae the terrace lines run forward and outward, and on the outer parts they swing more strongly outward. Two of them are better developed than the others, and, running parallel with the margins, reach the extremities of the pleurae (pl. 2, fig. 5). In addition, slight ridges bound the edges of each pleura, the anterior one being the stronger.

The anterior thoracic segment is greatly modified. A large modification of the adaxial part of the leading edge produces an upflexed articulatory band which lies against the similarly shaped posterior edge of the fixed cheek. Behind this a strong furrow is present. Lateral to it the upper surface of the pleura tapers much more rapidly than do the succeeding pleurae, and on the anterior face a broad transversely (tr.) striated facet is present. The striae fan out slightly laterally, that is, they are more widely spaced near the tip of the pleura, where they number ca. 8 per 0.5 mm.

The most similar described species from overseas is Kosovopeltis svobodai Šnajdr, but K. svobodai can be distinguished by its wider fixed cheeks, relatively smaller palpebral lobes, fine terrace lines on the glabella, and more angular anterolateral corners on the pygidium. In the North American Silurian only two other species can be confidently referred to Kosovopeltis. One, K. acamus (Hall) from the Racine Dolomite (Wenlockian-lower Ludlovian) of Wisconsin, has a cranidium of similar shape to that of K. nebula, comparable glabellar furrows, and a wide pygidial doublure. However, it differs in its slightly wider fixed cheeks, less sharply defined pygidial axis and pleurae, and more elongate outline and more angular anterolateral corners of the pygidium.

The species from the Upper Silurian at Port Daniel, Gaspé, described by Billings (1863) and Northrop (1939) as Bronteus pompilius and Goldius pompilius, respectively, also probably belongs in Kosovopeltis (see Whittington, 1960, p. 415, who has used the specific name, correctly, for Billings' material from the Lower Devonian of Square Lake, Maine). By courtesy of C. Mac-Clintock, I have been able to examine Northrop's specimens. The glabella does not differ in any significant way from that of Kosovopeltis, there is no preglabellar furrow, the eyes are large and situated well back, the pygidium is semielliptical in outline and has a doublure that is 0.60 to 0.65

of the postrhachial length, and the ornament of the pygidium consists of terrace lines and delicate pustules.

Scutellum rochesterense Howell and Sanford, from the upper Llandoverian-Wenlockian Iron-dequoit Formation of New York, apparently belongs to the genus *Planiscutellum* Richter and Richter.

Kosovopeltis bypha, new species Pl. 1, figs. 1-7; pl. 3, fig. 3

Types.—Holotype OU 4964A and paratypes OU 4964B-D and OU 5622A, B, from near C sec. 4, T. 2 N., R. 6 E., Pontotoc County.

Description .- Known from thorax and pygidium only. Thorax with nine segments visible, but there could be a tenth; axis broad, moderately arched; axial furrows distinctly impressed and unornamented; in lateral profile rings arch from the back in a broad curve into the deep articulating furrow; articulating half rings rise abruptly from the furrows and arch gently on their crests; in longitudinal section (exsag.) pleurae between axial furrows and fulcra have steep slopes back and front and a somewhat flattened crest; no sign of pleural furrows; lateral to the fulcra pleurae curve slightly backward and become sabre-shaped in outline, and progressively more flattened in profile apart from a narrow but prominent ridge on the leading edge. Ornament on rings consisting of terrace lines of two types—a basic set more or less regularly arranged in arcs of circles with the posterior edges of the rings as chords, and a much less persistent irregular set forming small arcs generally transversely (tr.) arranged; in a narrow band adjacent to the axial furrows only the first set is developed; across the posterior edge of each ring one or two fine, almost continuous transverse lines present; articulating half rings with strong transverse terrace lines on the posterior half, and anterior half almost smooth; pleurae adaxially to fulcra with anastomosing lines directed forward and slightly outward, and with the degree of anastomosis greatest along the posterior crest of each pleura; abaxially to fulcra, on the posterior edge of each pleura, terrace lines form progressively stronger hooks convex to the axis, until the hooks become invaginated and form a pair of parallel terrace lines along the posterior edge with short lines at right angles between them; over remainder of pleurae terrace lines run forward and outward toward the anterior border where they condense to form a distinct "plaited" ridge.

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Well-preserved pygidia, ranging from 28 to 42 mm in width, and fragments of individuals, from 13 to 55 mm wide, are available; shape, number and arrangement of pleurae, and shape of axis all similar to Kosovopeltis nebula except for a wider range in length/width ratios (0.65 to 0.75), and a median furrow in the posterior pleura (former could be due to wider range in size). Ornament distinctive — at all growth stages, considered over the whole pygidium, the terrace lines markedly convex to the rear, and on anterior pleurae directed forward at more than 45° to the anterior edge; in juveniles (13 mm wide) 14 to 18 lines per mm on the median pleura, which at that stage is undivided; at width of 30 mm, 14 to 18 lines per mm on the central part of the pleurae but near the rear every second line not developed, leaving 7 to 9 lines per mm, and around the axis a complex "fingerprint"-type ornament present; at greater widths area of "fingerprinting" occupies one-half to two-thirds of the pleurae, becoming less strongly marked away from the axis, and the simple lines near the rear number 4 to 5 per mm; at least at width of 26 mm and above, axis with "fingerprint" terrace lines; axis not known from smaller specimens. Doublure widest posteriorly; measured along the first pleural furrow, doublure about one-half the distance from margin to axial furrow; along posterior pleura, figure the same though posterior pleurae much longer than anterior ones; pattern of terrace lines on doublure not clear, but lines spaced ca. 2 per mm near the inner edge and 5 per mm near the outer edge on a specimen 36 mm wide; on outer two-thirds of doublure lines swing outward beneath the pleural furrows, amount of swing increasing toward the margin.

Remarks.—As noted above, the absence of the cephalon makes the generic identification difficult. Using the criteria of Šnajdr, however, no known feature would exclude it from Kosovopeltis. It can be distinguished from K. nebula by constant differences in the patterns of terrace lines on the thorax and on both the dorsal and doublure surfaces of the pygidium, the median furrow on the pygidium, and the width of the pygidial doublure. The two species apparently occur together, and similarities in outline, profile, plan and cross section of the pleurae, position of the fulcra, and organization of the axis of the pygidium are so great that one is forced to entertain the possibility of sexual dimorphism. If dimorphism were established, a reassessment of taxonomically significant characters in the group would be necessary.

Knowledge of the cephalon of K. hypha is needed before a complete discussion is possible. The naming of the two as separate species herein is not intended to prejudge the issue, but rather to point up the morphological differences which, upon the basis of most recent work, would indicate that they are specifically distinct.

Family PROETIDAE Hawle and Corda, 1847 Subfamily PROETINAE Hawle and Corda, 1847

Genus Proetus Steininger, 1831

Type species.—Proetus concinnus (Dalman), from the Mulde marl (Wenlockian) of Gotland.

Remarks.—Proetus has been the subject of numerous diagnoses and discussions in recent years (Erben, 1951; Kielan, 1954; Richter and Richter, 1956b; Přibyl, 1946, 1958, 1964; Whittington and Campbell, 1967). It is difficult to set meaningful morphological and stratigraphical limits to the genus, but it should be noted that there is a clear-cut group of Ludlovian species including P. concinnus (Dalman), P. fletcheri Salter, P. morinensis Přibyl, P. pluteus Whittington and Campbell, P. foculus, new species, and possibly P. latifrons (McCoy). This group is characterized by fine granulation of the glabella, the presence of prominent genal spines, fine pitting on the free cheeks inside the border furrows, the absence of a true border furrow on the pygidium, and the continuation of the marginal terrace lines on the pygidium inward toward the axis. These characters taken individually are apparently of minor importance, being details of ornamentation. However, the present data suggest that together they define a stratigraphically significant group. If this possibility is confirmed by subsequent work, it may be worth according the group subgeneric status.

Proetus foculus, new species Pl. 4, figs. 1-12

Types.—Holotype OU 5610, from SE 1/4 SW 1/4 sec. 4, T. 2 N., R. 6 E., Pontotoc County; paratypes OU 5611, from SE 1/4 SE 1/4 sec. 4, T. 2 N., R. 6 E., Pontotoc County, and OU 5612, from Vines Dome, NW 1/4 NW 1/4 sec. 2, T. 2 S., R. 2 E., Murray County.

Description.—Excluding the genal spines, cephalon almost semicircular; glabella ca. two-fifths

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the width of the cephalon, widest at the posterior border, narrowing rapidly across the occipital ring, then more gradually toward the well-rounded anterior; glabella reaches anterior furrow; axial furrows lightly impressed, and rise at ca. 70° to the rear and ca. 50° to the front of the palpebral region; occipital furrow with transverse lateral sectors extending one-quarter the width, and a forwardly arched and shallower central sector; faint furrow running posterolaterally from the flexure points of the occipital furrow and dividing off the slightly inflexed ends of the occipital ring; no other glabellar furrows present; in lateral profile occipital ring (apart from the slight median node) highest at the rear and drops in a sharp arc to the occipital furrow, while the remainder of the glabella forms an even arc ca. seven-tenths as high as it is long; palpebral lobes well rounded in outline, as high as the central part of the glabella, and ca. three-eighths as wide (tr., measured from the axial furrow) as long (exsag.); distance between outer tips of palpebral lobes (tr.) approximately equals length of cephalon (sag.); visual surface sausage-shaped, delineated below by a slight but distinct furrow, and surmounting a socle ca. one-quarter its own height; cheeks broadly convex inside border furrows; posterior border furrows narrow, rather sharply incised and straight, apart from a slight forward swing at their outer ends; lateral border furrows much broader and rounded, joining the preglabellar furrow in front, and passing backward a very short distance beyond the ends of the posterior border furrows; lateral and anterior borders rolled around to doublure; genal spines extending back only ca. 3 mm beyond the posterior border furrow on a specimen with glabella 6.5 mm wide; doublure rising steeply in front, and progressively less steeply toward the genal angles; facial suture with ω a short distance inside the genal spine; posterior to the eye it lies close to the axial furrow and runs posterolaterally to the border furrow where there is an angle, and then straight to ω ; γ only 0.3 mm from axial furrow; γ - β only slightly curved, with β well out on the border; β - ρ - ρ - β forming an almost continuous curve, but broken by a slight angle at ρ ; rostral suture situated just below the anterior margin but nevertheless visible in direct anterior view; rostral plate triangular in outline and stands almost vertically; on ventral surface below ω suture passes across the inner edge of the genal spine.

Ornament on glabella consisting of a small median occipital node, and probably fine granula-

tion; cheeks posterolateral to the eyes with faint irregular reticulate markings, probably genal caecae; terrace lines on lateral and anterior borders; they are more widely spaced (4 per 0.5 mm) on the upper than on the outer (7 to 8 per 0.5 mm) surface, measured in front of the genal spine; terrace lines on doublure ca. 5 per 0.5 mm.

Thorax with ten segments; axis highly and regularly arched, and more than one-third the thoracic width (tr.) at all segments; axial furrows lightly impressed; rings with preannulus and articulating half ring normally developed; no true intra-annular furrow present, only a change in slope; articulating furrow deep, well rounded, and continuous to the axial furrow; postannulus equal in length (sag.) to the remainder of the segment; in anterior profile pleurae evenly arched, no break in slope at the fulcrum; pleural furrows moderate, almost straight in dorsal view, but bent back slightly near the fulcra, and run a short distance down onto the facets; fulcra prominent; pleural tips abruptly truncated; near the tips the posterior edge of the facet with a terrace line, and several other terrace lines join it at a focus in the posteroventral corner (pl. 4, fig. 11); on enrolled specimens, terrace lines along edge of pleura in line, presumably making a tight closure with the terrace lines on the cephalic doublure; ventral surface of thorax unknown.

Pygidium with nine rings (last two almost imperceptible) and 6 + 1 pleurae (last three almost imperceptible); outer margin a continuous curve; width approximately twice the length; axial furrows scarcely impressed but marked by an abrupt change in slope from the gently arched pleurae to the highly and evenly arched axis; in lateral profile anterior ring much more prominent than all subsequent ones and slopes down to the half ring in front and more sharply to the second ring; second and subsequent rings tending to be flattened on top (in lateral profile) and with a vertical step-down at the rear; slight external swelling in the posterolateral corners of each of the first five or six rings, presumably marking the positions of muscle insertion beneath; first five interpleural furrows terminate axially against their corresponding ring furrows but position of subsequent ones not determinable; from ca. 0.5 mm out from the axial furrows to a line corresponding with the inner edge of the doublure, the rear edges of the pleura with fine raised flanges sharply delineating the interpleural furrows; above the doublure the interpleural furrows broad and shallow, and almost indistinguishable; pleural furrows not

quite reaching the axial furrow and deepest behind the fulcra; 0.5 to 1 mm inside the doublure edge a "terrace line" develops along the anterior edge of each pleural furrow and runs to the margin, dividing the pleura into posterior and anterior bands of approximately equal width; outer half of each anterior band diagonally subdivided by another terrace line; terrace lines take a sharp posterior swing at the border and form a series of lines parallel with those on the doublure; fulcrum on first pleura prominent; no border present and only a faint break in slope of the surface over the inner edge of the doublure; doublure bent in sharply at the margin, has a gently rounded outer band, and a flatter, more steeply inclined inner band.

Remarks.—Proetus foculus, new species, is not far removed from P. concinnus (Dalman), the type species. Differences are in the less inflated glabella of P. foculus in both lateral and longitudinal profile, its relatively broader and less highly arched axis on the thorax, greater postannulus-to-preannulus ratio, and relatively broader pygidium. P. conspersus Angelin from the Klinteberg Formation (Ludlovian) of Gotland has a more elongate fiddle-shaped glabella and is more coarsely ornamented than the above species. A Ludlovian species from Czechoslovakia, P. morinensis Přibyl from the Kopanina beds, has affinities with P. concinnus, but it too has a more convex glabella and axis than has P. foculus, and has pygidial axial rings which are more arched in longitudinal profile. The relations beteween P. foculus and P. pluteus Whittington and Campbell, from the Hardwood Mountain Formation of Maine, have been discussed previously (Whittington and Campbell, 1967, p. 456).

Family CHEIRURIDAE Hawle and Corda, 1847

Subfamily CHEIRURINAE Hawle and Corda, 1847

Genus Cheirurus Beyrich, 1845

Type species.—Cheirurus insignis Beyrich, from the Wenlockian of Czechoslovakia.

Remarks.—Cheirurus is interpreted in the sense of Prantl and Přibyl's (1947) interpretation of the subgenus Cheirurus (Cheirurus). An adequate diagnosis is given by Henningsmoen in Harrington and others (1959, p. 431).

Range.—Late Ordovician-Silurian.

Cheirurus infensus, new species
Pl. 4, fig. 13; pl. 5, figs. 1-12; pl. 6, figs. 1-10;
pl. 7, figs. 1, 2; text-fig. 2

Types.—Holotype OU 5604 and paratypes OU 4968A-C, OU 5606, and USNM 153145, from C sec. 4; paratypes OU 5608A-C, from C SW 1/4 sec. 4, and paratype OU 5605, from C NW 1/4 sec. 4; all in T. 2 N., R. 6 E., Pontotoc County.

Other material.—Five incomplete specimens from the holotype and paratype localities and two from Murray County, one from SW 1/4 SE 1/4 sec. 17, T. 2 S., R. 1 W., and the other from NW 1/4 NW 1/4 sec. 2, T. 2 S., R. 2 E.

Description.—Cephalon almost semicircular in outline, the posterior edge forming the diameter; sweep of the anterior edge broken by the distinct forward projection of the glabella; glabella expands considerably toward the front, the maximum width being about half way along the frontal lobe; ratio of occipital width/maximum width of glabella ca. 2:3; expansion of the glabella stepwise, the occipital and 1p lobes expanding at a more or less constant rate, 2p and 3p at a slightly greater rate, and the frontal lobe at a still greater rate; axial furrows only lightly impressed. Outer parts of occipital furrow transverse, short (exsag.), and sharply down-folded into apodemes; axially, furrow broader, much shallower, and bent forward in a sweeping arc; occipital ring is ca. one-sixth (sag.) the length of the glabella; furrow 1p straight or slightly arched, in outer course deeply incised to form apodemes, and axially shallowing abruptly approaching the nexus with the occipital ring; furrows 2p and 3p short, and not so deeply incised; both slightly arched, approximately transverse, and extend ca. one-third the distance across the glabella; furrow 2p at approximately the midlength of the glabella; measured along the axial furrows, ratios of the lengths occipital ring/lobe 1p/lobe 2p/lobe 3p ca. 5:12:-6:7, with only slight variation in this character in four specimens of glabellae having lengths from 20 to 25 mm; palpebral lobes slightly but abruptly raised above the surrounding area, subtriangular in outline, and situated with their midpoints opposite furrows 2p; no whole eye surfaces preserved, but the contours of the base of the eye suggest a gently convex structure of about the same length as lobe 3p.

Posterior border gently rounded and almost parallel-sided, but the outline broken by the fulcral articulatory apparatus, at which point there is also an abrupt change in slope (tr.); posterior border furrow opposite end of occipital furrow, much narrower than posterior border, well rounded in section, and tapering in length (exsag.) slightly at each end; lateral border forming a well-rounded roll uniform in width except as it approaches anterior branch of facial suture, then expanding slightly before tapering away on front of the glabella; no anterior border present, glabella descending onto the rostrum with only the faintest change in slope; no true border furrow present, the cheeks descending gently to an abrupt rise at the edge of the border; genal spines robust, gradually tapering, higher than wide, curved slightly upward and inward, and extending back beyond the third thoracic segment.

Ornament on the glabella of two types—near the median posterior margin of the occipital ring, 4 to 6 small, sharp, irregularly placed pustules; very delicate granules numbering 30 to 40 per sq mm on the median part of the glabella in front of furrows 1p and running forward to cover an expanding area on the frontal lobe; remainder of the glabella smooth.

Cheeks inside the borders ornamented with shallow pits, circular to radially ovate in outline, smallest near the axis and behind the eyes, and gradually increasing in size anteriorly and laterally; narrow palpebral lobes and a narrow strip running from them to the prominence against furrow 3p, and thence forward to the front of the glabella, free of pits; posterior borders smooth, but lateral borders and genal spines finely and densely granulated on both upper and lower surfaces.

Facial sutures run around the front edge of the glabella and join the rostral suture, which is approximately equal in width (tr.) to the occipital ring; β - γ slightly divergent from the axial furrow; γ between furrows 2p and 3p; suture runs outward and slightly forward from ϵ to the border furrow, then cutting back sharply across the border and around under the base of the genal spine; connective sutures cut backward and inward, and isolate a rodlike rostral plate; hypostomal suture forming an arc of a circle with its ends situated immediately beneath the widest part of the glabella.

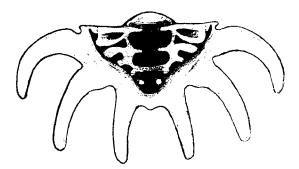
Hypostome of the usual general shape for the genus; maximum width of the whole structure at the anterior wings, and of the central body slightly in front of this; tips of the anterior wings at approximately the midlength of the hypostome; posterior outline squarish with a shallow median embayment, and the faintest suggestion of a spine at each corner; lateral outline behind the shoulder distinctly concave; anterior border narrowing rap-

idly from the anterior wings to a point just within the maximum width of the central body, then more gradually; border continuous around the whole anterior margin although becoming almost linear; anterior furrow narrow and deep (even slightly recessed) in front of the wings, but also shallow and linear in front; lateral borders of almost uniform width, except toward the rear where they expand considerably; borders roll over in a broadly rounded manner to the posterior wings, but toward the rear roll progressively more sharply; posterior border flattened or gently convex; lateral and posterior furrows well rounded, not of uniform depth, but with a pronounced deepening between the shoulder and the macula, and a smaller one in the posterolateral corners; maximum convexity of the central body in the anterior half; middle furrow shallow; surface of macula flattened and smooth; a pair of similar smooth structures on each flank of the central body in the depression of the lateral furrow; on whole central body and on median part of posterior border irregularly shaped and arranged slightly depressed areas present, darker in color than the remainder of the test, and in fact resembling the maculae in color (see Lindström, 1901, p. 49-50); hypostomal ornament granular, but not uniform; on anterior half of central body coarser granules scattered through finer ones; on lateral and posterior borders granules coarser than those of central body, and themselves becoming coarser from back to front; in lateral furrows granules similar to those of central body in size, but those near the shoulders slightly elongate; those on the anterolateral borders and wings fine and widely spaced; doublure of the normal shape for the family, except that the posterior wings extend farther inward than usual.

Number of segments in thorax unknown; axial rings all distinctively humped, that is, flattened on the flanks and rather sharply arched in the middle; an irregularly arranged group of tubercles (5 to 6) on the median posterior part of each ring; longitudinal profile of rings as shown in plate 6, figure 2; highest point in all cases near rear edge, and a sharp drop into articulating furrow from both front and back; apodemal pits deep, more open at each end than in the middle, set at 15° to 20° to the width of the segment, with their posterior edges behind the posterior edge of the articulating furrow; articulating furrow crescentic in plan with the tips of the crescent at the ends of the apodemal pits; axial furrows pronounced; pleurae of the usual shape for the genus; their tips

crushed in most specimens and not well preserved, but both leading and trailing edges granulate, and central parts smooth.

Pygidium large with the axis moderately arched in front and rapidly diminishing in height posteriorly; three axial rings distinct, and a fourth indistinct; axial furrows distinct at the first ring, barely visible at the second, and not present subsequently; anterior edge (excluding the articulating half ring) almost straight between the fulcral facets, but outside these deep notches present at base of first marginal spines; articulating half ring equal in length to first ring; deep slits forming apodemes similar to those of the thorax present on the first and second rings, the third with a much reduced shallow ovate pit producing an almost imperceptible swelling on the ventral surface, and the fourth with no structure at all; first pleural segment clearly defined posteriorly by a transverse furrow sharply incised axially, but tending to arch backward and fade away laterally; large highly curved spine, circular in cross section, formed from first segment; short sharp pleural furrow similar to those of the thoracic segments present; boundary between second and third pleurae not marked by a furrow, but the pleural furrow of the second segment is longer (exsag.) and comparable in depth with that of the first; second spine a little longer than the first, and much less arched; pleural furrows of the third and fourth segments pitlike, and both produce apodemelike prominences on the ventral surface (possibly they took over the function of muscle attachment as the three apodemes atrophied); third spine slightly shorter than the other two, only gently flexed, and at a low angle to the axis; short well-rounded medial posterior projection probably representing the unseparated fourth spines, but showing no



Text-figure 2. Ventral surface of a pygidium, x1.9, of Cheirurus infensus, new species, showing the apodemes on the first and second segments and the apodeme-like modifications of the pleural furrows of the third and fourth segments.

sign of a median division; spines directed upward at angles of 20° to 30° to the general plane of the doublure, the angle increasing with successively posterior spines; doublure well rounded in section with its inner surface standing almost vertical; deep posterior embayment in doublure exposing the eminences from the fourth pleural furrows, and producing an arch in posterior profile. The ornament is poorly preserved on the available specimens. At least the first two axial rings apparently with sharp irregular pustules similar to those of the thoracic rings; spines completely covered with fine granules of the same type as those on the genal spines and doublure.

Remarks.—Cheirurus infensus is readily distinguished from the type species, C. insignis, by the following features: the shallower indentation in the anterior outline at the outer edge of the glabella; the finer ornament on the glabella; relatively wider anterior lobe on the glabella; longer more robust genal spines; less convergent anterior limbs of the facial sutures; longer, narrower, and more nearly circular (in section) spines of the pygidium; short median projection of the pygidium; and finer ornament, more definite posterolateral and posterior border furrows, and broader borders on the hypostome.

Similar features distinguish it from the Barrandian C. obtusatus Hawle and Corda, and the British C. bimucronatus (Murchison). The other species from Europe have distinctively modified postaxial parts on the pygidium.

Raymond (1916) reviewed all the known American Silurian members of the genus as he understood it. Since then no new Silurian species has been described, with the possible exception of Cheirurus singularis Howell and Sanford, 1947, the generic position of which is doubtful, as the pygidium is unknown. Each species discussed by Raymond presents a problem. The types of C. niagarensis need clarification; the pygidia of C. welleri, C. dilatatus, and C. patens are not definitely known; and the exteriors of the cranidia on which C. patens and C. welleri are based have not been described.

The whole group of American Silurian cheirurids is in need of revision before detailed comparative work can be undertaken, and this revision will require extensive recollecting. However, it is possible to distinguish *C. infensus* from all existing species upon the basis of the information available. *C. welleri* Raymond has a narrower glabella, more pronounced furrows 1p and 3p, and less robust genal spines. Both *C. patens* Raymond and

C. dilatatus Raymond have narrower cheeks relative to the glabella and more pronounced furrows 1p-3p, and, in addition the latter at least, has coarser ornament on the glabella and short rather flat spines on the pygidium. Assuming the validity of Raymond's argument (1916, p. 30-32) that the types of C. niagarensis are from the Rochester Shale, that species has more pronounced glabellar furrows, relatively shorter genal spines, larger granulations with large perforations distributed over most of the glabella including the lateral parts of the glabellar lobes, a more coarsely ornamented hypostome, and relatively shorter and flatter spines on the pygidium.

The material from the St. Clair Limestone of Arkansas that has been assigned to *C. niagarensis* (van Ingen, 1902) is almost certainly another species characterized by still coarser perforated granules over the entire glabella (including the occipital ring). However, its pygidium is very close to that of *C. infensus*, particularly in the shape and disposition of the spines.

Cheirurus tarquinius Billings from the Gaspé area is also similar in many respects. However, it shows a less expanded anterior glabellar lobe; more scattered and rather larger granules on the glabella extending down almost to the anterior furrow; a genal spine with a sharp crest and a flattened dorsolateral face; a more rounded posterior edge on the hypostome; a relatively shorter median pygidial spine; and probably flatter lateral spines on the pygidium, although it is difficult to be sure of this because of distortion. The lectotype, of C. tarquinius (GSC 3081) is a broken cranidium on which the surface details are preserved in part. I have examined it and the material illustrated by Northrop (1939), together with other material from Port Daniel, housed in the Peabody Museum at Yale University.

Genus Anasobella, new genus

Type species.—Anasobella asper, new species, from the Henryhouse Formation of Oklahoma.

Diagnosis.—Small for the subfamily; glabella expanding and strongly convex; furrows 2p and 3p short, 1p strong and transverse; midpoint of eyes opposite 1p; genal spines short; hypostome flattened, with a posteriorly tapering central body, and anterior wings at one-third the length from the front; thorax composed of ten segments; pygidium with three short flattened marginal spines on each side and a very short median spine.

Remarks.—Anasobella, new genus, has some

affinity with Pseudocheirurus Prantl and Přibyl, 1948, in the short genal spines and the short flattened pygidial spines. The characters of the cephalon, however, are quite distinct. In particular, the degree of inflation and expansion of the glabella, the shorter, less oblique furrows 2p and 3p, the strongly incised transverse furrow 1p, the larger more posterior eyes, the posterior position of ω , the deeper axial furrows, and the more tapering central body and more posterior anterior wings of the hypostome characterize Anasobella. Although in the Cheirurinae the number and shape of the pygidial spines have been used as guides to relationship, and glabellar characters are allowed considerable latitude within a genus, the features listed above together have such weight that it is unreasonable to deny them generic value. This judgment is confirmed by the existence of only ten thoracic segments in Anasobella as opposed to eleven in Pseudocheirurus.

It should be noted that, in erecting this new genus, one is merely assigning taxonomic values to morphological features in the fashion currently accepted by workers on cheirurids. No attempt has yet been made to analyze the morphology, stratigraphy, and geography of the family as a whole, and therefore the existing generic subdivision lacks an adequate theoretical basis. This basis cannot be provided until the Silurian and Devonian cheirurids are known in the same detail as are the Ordovician ones. The establishment of Anasobella may help toward this end.

Range.—The genus is known only from the Henryhouse Formation.

Anasobella asper, new species Pl. 7, figs. 3-14

Types.—Holotype OU 5646, from bench above stream near C sec. 10, T. 2 N., R. 6 E., and paratype YPM 24880, from NE 1/4 sec. 9, T. 2 N., R. 6 E., both in Pontotoc County.

Description.—Larger specimen (holotype) about 25 mm long when extended; cephalon semicircular in outline; lateral glabellar profile, excluding the occipital ring, almost a quadrant of a circle; glabella expanding to the front, with a maximum width at the frontal lobe and minimum at the occipital ring—maximum/minimum width about 3:2; occipital furrow deep and joined medially by the strong furrow 1p to form a deep well-rounded trench; furrow 1p only moderately oblique laterally, transverse medially; furrows 2p and 3p slightly curved, extending ca. one-third of the

distance to the midline, deep laterally and shallowing rapidly, but evenly, medially. Border furrows deep, with lateral furrow more open than the posterior one; posterior border same length (exsag.) as lateral part of occipital ring; lateral border more gently arched and twice the dimensions of the posterior; genal spine depressed ovate in section and shorter than the occipital ring. Palpebral lobe raised, but lower than the crest of the glabella, separated from the fixed cheek by a strong wellrounded furrow, and with its midlength opposite the outer end of furrow 1p; eye and palpebral lobe together almost hemispherical; visual surface of eye sausage-shaped and surmounting an almost vertical socle ca. half its own height. Facial suture with ω opposite the midlength of the posterior border, arching forward across the lateral border, then transversely to ϵ ; both ϵ and γ nonangular, but γ a much gentler curve than ϵ ; suture in front of ϵ close to the axial furrow and gradually converging to it; rostral suture touching the preglabellar furrow medially; rostral plate equal in width to the glabella at lobe 1p; connective sutures strongly convergent.

Surface of glabella with scattered granules 0.07 to 0.15 mm in diameter, the smaller ones, in general, toward the front; no granules on glabellar lobes; single median node on occipital ring; a few granules similar to those on glabella on free cheek below the eye on the paratype, and a few more on the crest of the lateral border; closely packed granules on outer face of borders and on rostral plate; coarse scattered pits over inner cheeks and extending down into lateral border furrows.

Hypostome poorly preserved; lateral profile rather flat; less than half as wide at the posterior margin as at the shoulders; lateral and posterior borders broad and flat; anterior wings dividing the length in the ratio of ca. 1:2; median body tapering rapidly to a well-rounded posterior.

Thorax of ten segments; axial furrow lightly impressed; rings moderately arched, bent forward distinctly at their ends; articulating half rings long, almost vertical at the back and more gently sloping in front; rings dropping gently toward the front; articulating furrow incised. Pleura swollen adaxially, then wasting away toward the fulcrum and expanding to form a generally lanceolate spine; no longitudinal furrow along the pleurae in line with the fulcra; pleural furrows short (tr.) and shallow, reaching only two-fifths of the distance from the axial furrow to the outer ends of the fulcra; well-developed articulating facets developed on both anterior and posterior

edges of pleurae, extending as narrow shelves right to the axial furrow; pleural spines produced to a point on most segments, but posterior three progressively more blunt, and resembling the spines of the pygidium; dorsal surface apparently smooth, but slightly worn.

Pygidium with poorly defined axial furrows; three complete axial rings distinctly arched forward, and a tiny ill-defined terminus; apodemal pits elongate at first segment, circular at the last; interpleural furrow clear between first two segments, but indefinite subsequently; faint pleural furrow on first segment only; pleural spines short and flattened, and subrectangular in outline; doublure with a deep median embayment; dorsal surface apparently smooth; ventral surface of spines finely granulate.

Remarks.—Only two specimens are known, but both are well preserved and show most of the characters. The paratype would be ca. 19 mm long if straightened.

Family ENCRINURIDAE Angelin, 1854

Subfamily ENCRINURINAE Angelin, 1854

Genus Fragiscutum Whittington and Campbell, 1967

Type species.—Fragiscutum rhytium Whittington and Campbell, from the Hardwood Mountain Formation (upper Wenlockian or lower Ludlovian) of Maine.

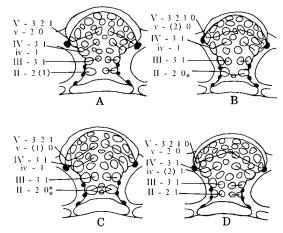
Remarks.—Fragiscutum is apparently restricted to North America, and at present is known only from the type formation and from the Henryhouse.

Fragiscutum glebalis, new species

Pl. 8, figs. 1-19; pl. 17, fig. 14; text-fig. 3

Types.—Holotype YPM 24881, from NE¹/₄ sec. 9; and paratypes OU 5638, OU 5641, OU 5644, from SE¹/₄ SW¹/₄ sec. 4; USNM 153146-47, from near C sec. 4; OU 5643, from NE¹/₄ SW¹/₄ sec. 10; OU 5793, from C sec. 10; all T. 2 N., R. 6 E., Pontotoc County. Paratypes OU 5639, from SW¹/₄ SE¹/₄ sec. 17, T. 2 S., R. 1 W.; and OU 5640, from SE¹/₄ NE¹/₄ sec. 28, T. 1 S., R. 2 E.; both Murray County.

Description.—Exoskeleton small for the family; viewed ventrally margin of cephalon parabolic in outline; anterior outline broken by strongly pro-



Text-figure 3. Variation in the tubercle pattern on the glabella of Fragiscutum glebalis, new species. Tubercles numbered according to Tripp (1957). Note that alternative interpretations could be given for some tubercles; e.g., in figure D, row iv could be read as 1, 0 rather than (2), 1. No tubercles shown in front of facial suture.

jecting glabella; axial furrows deep and broad; width of occipital ring ca. 0.35 of maximum cephalic width; glabella tapering rapidly in front of occipital ring, narrowest at lobe 1p, and expanding to a well-rounded anterior; ratio of width at occipital ring/width at lobe 1p/maximum width ca. 11:6:15; occipital ring short (exsag.) behind the apodemes, expanding to double this length medially; furrows 1p deeply indenting the glabella and running into the occipital furrow, thus isolating a minute lobe 1p; furrow 2p complete, forming deep indentations laterally; lobe 2p with four tubercles, sometimes compound; furrows 3p and 4p indenting the glabellar margin; anterior pit deep; true preglabellar furrow weak; false preglabellar furrow close to the anterior border and also weak; basic tubercle formula for glabella, II - (0*), (1), 2; iii - (0); III - 1, 3; iv - (0, 0, 0), (1), (2); IV -(0), 1, (2), 3; v - (0); V - 1, (2), (3); VI - 1, 2; palpebral lobe semielliptical in dorsal view, rising up almost vertically from the axial furrow in front and from the platform of the fixed cheek at the back; tips of palpebral lobes bent over almost to the horizontal, and bearing a pronounced pit; eye and palpebral lobe form a hemisphere on a slight socle, but not pedunculate; lateral and posterior border furrows deep, but both shallow toward the genal angle; cheek platform inside border furrows high and bearing a few coarse irregularly arranged tubercles; tubercle ring broken at the anterior of the palpebral lobe; posterior border short (exsag.) from axis to fulcrum, expanding slightly laterally

to a small blunt fixigenal spine; lateral border steep, only gently convex; tubercles present only on genal extremities of posterior border, but broad, low tubercles present around entire lateral border. Facial suture with ω just inside genal angle, running straight forward on the border for a short distance, then swinging in abruptly; ϵ broadly rounded; δ lateral to an exsagittal line through the widest part of the glabella. Rostral plate broadest at anterior margin and tapering slightly and irregularly toward the hypostomal suture; almost twice as high as wide. Ventral edge of border narrow but in many cases bearing a shallow vincular furrow laterally; doublure vertical.

Tubercles on the glabella with as many as five perforations (usually one to three); other cephalic tubercles also probably perforate but in most cases not clearly so; lateral borders, region in front of pseudo-preglabellar furrow, and tubercles on glabella in front of palpebral lobes, covered with fine granules. Hypostome as wide as long and extending back beyond the posterior edge of the cephalon; central body large, rhombic in outline and approximately three-fourths the total length of the hypostome; median lobe relatively narrow, not sharply separated from surrounding area by abrupt changes in slope or by furrows, and stopping well short of the anterior margin; macula small, smooth, faintly swollen; anterior border slightly thickened and turned ventrally; anterior border furrow narrow and sharp; lateral border narrow, and lateral border furrow deep and slightly overhung by the median body; posterior border approximately onefifth the total length of the hypostome, and tending to be slightly pointed posteriorly; posterior border furrow not as deep as lateral furrow, not incised; anterior wings situated just forward of the midlength, their detail not preserved; posterior wings not well preserved but prominent; lateral doublure narrow; posterior doublure stops short of median body; median body and posterior border covered with fine granules.

Ten segments in thorax; shape and structure of segments as in F. rhytium Whittington and Campbell, except for slightly shorter pleural spines; surface apparently smooth, but slightly weathered specimens with as many as forty perforations arranged in an irregular row along the crest of the posterior band on each segment.

Pygidium with 13 to 14 rings and 6 to 7 pleurae; more or less triangular in outline; width/length/height ratios are approximately 20:12:9; no mucro present—posterior end bluntly rounded;

first two rings continuous across the axis in all specimens, but as many as five in some; deep apodemal pits present on the anterior segments, situated well in from the axial furrow; posteriorly pits become shallow; median tubercles weak and number from three to seven; most common arrangement is four tubercles, one on each of rings 2, 5, 8, 11 (numbering from anterior); articulating half ring almost as long as remainder of first segment; first pair of pleurae tending to be flattened toward the axis in anterior profile, but curving over and dropping almost vertically on the flanks; the inner flattened zone diminishes rapidly posteriorly, and the more posterior segments curve steeply downward from the axis; in lateral profile anterior segments deflected slightly backward, but the degree of deflection increases gradually toward the rear; first two or three pairs of pleurae with differentiated posterior and anterior bands; on the first pair the flattened anterior bands, which form an articulatory surface, are only one-third to one-fifth of the length of the wellrounded posterior band; beyond the fulcrum, however, a broad anterior articulatory facet formed, separated from the posterior band by a sharp edge; on this facet, slightly forward of its midline, a distinct furrow which is a continuation of the furrow between the two bands further toward the axis; second and later pleural lobes well rounded, but with a steep posterior slope and a more gentle anterior one; interpleural furrows usually not distinguishable, but present as a subtle break in slope on the steep posterior slope of the posterior bands of the first few pleurae; pleural furrows deep and continued to the margin where the most anterior one is deeply incised, the degree of incision decreasing posteriorly; posterior pleural lobes forming sharp-edged flattened projections around the margins, but becoming less pronounced posteriorly and disappearing at the fifth lobe; no perforations have been detected in them; inside these projections a narrow smooth, granulated area present, more or less uniform in width except for a deep well-rounded indentation for the reception of the exterior bulge of the hypostome at the posterior end; inner edge of this granulated area projecting downward to form a pronounced rim; narrow smooth doublure bent back from this at more than 90°. Lateral parts of axial rings and crests of posterior pleural bands smooth or with almost indistinguishable eminences; irregular row of perforations along crest—five or six on each side of the anterior axial ring, and eight to ten on each anterior pleura.

Remarks.—The notation system originated by Tripp (1957, 1962) has been used for summarizing the tubercle system of the glabella. Seven specimens are well enough preserved to be used for this purpose. It is notable that no tubercles of rows I or ii are present in any specimen. The arrangement in row II is variable. In some individuals there is a single large tubercle on either side; in others there are two. Where a single tubercle is present, it may be double headed, indicating fusion. Tubercles 0 are variably developed. Attention is drawn to the point that II-0, should not be mistaken for I-0 as the furrow 1p clearly joins the occipital ring behind it. Row III is constant. In front of row IV it is difficult to distinguish any definite pattern on four of the seven specimens, and the formula given in the description should not be taken as typical.

Not all the glabellar tubercles carry a single perforation; some have two or three or rarely as many as five. Possibly the structures described as perforations on the thorax and pygidium do not reach the surface. They are best seen in worn individuals, and the size of the hole in the exoskeleton increases with the depth of wear. They are thus conical structures with upward-directed apices. The material is not well enough preserved to decide whether or not they penetrate the surface, but, if they do, the apertures are less than 0.05 mm in diameter.

Fragiscutum glebalis differs from F. rhytium, the only other known member of the genus, in having no tubercles between the palpebral lobe and the axial furrow, fewer and smaller tubercles in row IV and in the glabellar area in front of it, less distinct tubercles on the anterior and lateral borders, a relatively narrower posterior section of the glabella, wider axial furrows on the cephalon, less marked incisions on the hypostome around the anterior lobe, which extends further forward, and fewer pygidial pleurae.

The only described American species with which it could be confused (and then only with dissociated material) is *Encrinurus tuberculifrons* Weller. That species, however, has more numerous and smaller cephalic tubercles, a wider glabella posteriorly, tubercles between the palpebral lobe and axial furrow, and smaller eyes. The pygidia of the two species are more similar, but critical details are lacking. The thorax is unknown.

Family CALYMENIDAE Milne-Edwards, 1840

Genus Calymene Brongniart, 1822

Type species.—Calymene blumenbachi Brongniart, from the Wenlock Limestone of Dudley, England.

Remarks.—Calymene is here interpreted in the sense of Shirley (1936, p. 395). It thus contains a large number of species exhibiting a wide morphological range and covering the entire Silurian and the Lower and part of the Middle Devonian. It is possible to recognize species groups based upon certain characters within this complex, but the composition of the groups changes considerably according to the character or characters used; and no character, or group of characters, indicating lines of descent has yet been discriminated. A further difficulty is that insufficient morphological detail is available for many overseas species. It is suggested that, provided an adequate stratigraphic and geographic control is exercised, groupings within the genus (as at present understood) might best be sorted out by using the methods of numerical taxonomy (Sokal and Sneath, 1963).

Calymene clavicula, new species

Pl. 9, figs. 1-13; pl. 10, figs. 1-15; pl. 11, figs. 1-8; text-figs. 4, 5

Types.—Holotype USNM 153142 and paratypes USNM 153139-41, USNM 153143-44, and OU 5613-A, from near C sec. 4, T. 2 N., R. 6 E.; paratypes OU 5614, OU 5617, and OU 5619, from NW 1/4 SW 1/4 sec. 4, T. 2 N., R. 6 E. (Amsden's section P1); paratype OU 5616, from roadside near C W line NW 1/4 sec. 30, T. 3 N., R. 6 E.; all Pontotoc County. Paratype OU 5618, from SE 1/4 sec. 30, T. 2 S., R. 1 E. (Amsden's section Ca1(1), 1960), Carter County.

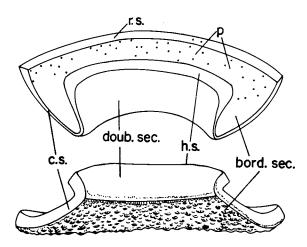
Other material.—Approximately 200 specimens from the holotype locality are in the collections of the U. S. National Museum and The University of Oklahoma. In addition to small quantities from the paratype localities, a few specimens have come from NW½ NW¼ sec. 5, T. 2 N., R. 6 E., and NW¼ NW¼ sec. 33, T. 3 N., R. 6 E., Pontotoc County.

The species also occurs in the Brownsport Formation in Tennessee. Specimen YPM 24877-79 is from near Linden, Perry County; USNM 158027 is from 70 feet above road in shaley bed on Indian Creek, 19 miles southeast of bridge over Indian

Creek on road to Martins Mills; USNM 158028 is from road cut on south side of U. S. Highway 70, 0.4 mile east of Harpeth River bridge.

Description.—Cephalon 3.6 to 3.9 times wider than long; anterior outline evenly rounded; posterior outline not straight but flexed backward slightly lateral to the fulcral points; glabella bellshaped with its sides tending to be subparallel in front of furrows 2p, and its anterior outline not evenly rounded but slightly flattened; widest part of glabella at, or slightly behind, lobes 1p; length/ width ratio of glabella (including occipital ring) 1.1:1.2. Axial furrows deep and steep-sided; in front of furrows 3p axial furrows of uniform width, but expand moderately at the border furrow; near lobe 1p axial furrows narrow and shallower than farther forward; occipital furrow longest (sag.) medially, becoming narrower laterally; glabellar furrow 1p deeply incised, directed backward and inward overall, its axial end bifid, with the main (posterior) branch flexed to lie at right angles to the median line, and the weak anterior branch directed forward and inward; "width" (exsag.) of the main furrow decreasing only slightly over its whole course; furrow 2p "narrow" (exsag.), directed inward and backward, and carried over in a weak depression to join the anterior branch of 1p, thus semi-isolating glabellar lobe 2p; furrow 3p lightly impressed, and directed upward or slightly forward; anterior pits shallow; occipital ring longest (sag.) medially, becoming rapidly shorter behind 1p, and then lengthening slightly again near the axial furrows; lobe 1p not distinctively shaped; lobe 2p crosses axial furrow with a buttress. Palpebral lobes situated opposite lobes 2p and almost flat or directed upward at a low angle; viewed anteriorly lobes on a slightly lower level than 2p. At axial furrow, posterior border approximately half the length of occipital ring, maintaining this length to fulcrum, then rapidly lengthening for about the same distance, and finally becoming more or less parallelsided near the facial suture; posterior border furrow deep, asymmetrical in longitudinal section, with the anterior slope gentle, and the posterior slope almost vertical (or even slightly overhanging) over much of its length, but becoming gentler laterally; furrow pinches out sharply near the facial suture. Facial suture with ω in the genal angle; ω - ϵ with a sharp flexure at the border furrow and a broad arc from there to ϵ ; only a slight curve at γ , but a subangular curve at β and α .

Visual surface of eye not preserved, but must



Text-figure 4. Reconstruction of the rostral plate, x5.2, of Calymene clavicula, new species, showing dorsal and posterior aspects. bord. sec. = border sector; c.s. = connective suture; doub. sec. = doublure sector; h.s. = hypostomal suture; p = perforations; r.s. = rostral suture.

have been steep, and crescentic in shape; narrow but prominent and distinctly convex socle below visual surface; cheeks strongly convex between socle and the deep V-shaped border furrow; furrow fading away abruptly approaching the facial suture back and front; border roll strongly rounded in profile near the genal angle, and progressively less rounded toward the front.

Rostral plate (as is normal for calymenids) divided into an outer sector forming part of the border roll, herein called the border sector, and an inner sector forming part of the doublure, herein called the doublure sector (Evitt and Whittington, 1953, p. 49-50); border surface gently convex in section (sag.), with its anterior edge forming an arc with a radius of ca. 12 mm, and its inner edge an arc of ca. 3-mm radius on a rostral plate 11 mm wide; ratio of length of chord of outer arc to chord of inner arc about 2:1; connective sutures slightly convex outward and strongly convergent in their course across the border sector, slightly divergent across the inner part of the doublure sector, and then convergent again toward the hypostomal suture; connective suture cuts vertically through the exoskeleton near the outer edge of the border sector, but becomes inclined inward and upward toward the doublure, almost vertical on the inner doublure, and inclined inward and upward toward the hypostomal suture; junction of the two rostral sectors angular and marked by a slight ridge; doublure sector with a steeply inclined posterior portion and a flatter anterior portion, which has a thin inner edge



Text-figure 5. Longitudinal profile of the glabella, x4.0, of Calymene clavicula, new species.

turned up to the hypostomal suture. Doublure of free cheeks steep, slightly concave and sharply flexed near the genal angles to receive the first thoracic pleura during enrollment (pl. 10, figs. 12-15); doublure of fixed cheeks downturned and with a strong articulating groove between the axial furrow and the fulcrum, but continuously expanding in length (exsag.) from the fulcrum to the facial suture.

Ornament on the glabella (except the occipital ring) and cheeks inside the border furrows (except the palpebral lobes) of pustules of various sizes up to 2/3 mm in diameter; no regular pattern in the arrangement of pustules of any size observed, apart from a general decrease in pustule size into the axial furrow and all the border furrows, which are smooth; posterior border between the axial furrow and fulcrum with pustules of medium size along its anterior slope and on its crest near the axial furrow, but lateral to the fulcrum with pustules similar to those on the cranidium, except on the almost-smooth posterior face; inner part of border roll with closely spaced pustules of medium size and circular outline, but outer part (including rostral plate) with pustules more elongate and crescentic in outline (progressively more elongate toward the genal angles), and with their dorsal edges sharp and steeply sloping, and their ventral faces flattened and gently sloping; doublure apparently smooth.

Hypostome of usual calymenid pattern (see Evitt and Whittington, 1953, p. 50-52); anterior border sharply flexed ventrally; anterior edge markedly embayed along the hypostomal suture; anterior wings deeply concave, and with a pronounced pit; lateral border furrow deep and fading away rapidly behind the posterior wings, but more sharply rounded behind them; median body evenly convex (tr.) anteriorly and posteriorly, but bearing a stout hollow spine medially; posterior border furrow shallow but sharp, and posterior border flattened and projecting into two prominent spines; median furrow faint, and running from a point on the lateral border furrow opposite the middle of the spine to a pair of large ovate maculae just behind the spine; doublure consisting only of a turned-down edge between the anterior and posterior wings, but behind the posterior wings consisting of a broad flap covering the posterior spines, and a narrow strip between; ornament much less pronounced than on dorsal surface of test; granules occur all over the borders, and on the central body, apart from the maculae, the median spine, and a pair of ovate areas anterolateral to the spine.

Thoracic rings highly arched, with slight swellings and slight forward flexure at each end; crests of rings also highly arched in lateral profile with a steep posterior slope throughout, but with a gentle anterior slope on the anterior rings becoming progressively steeper on posterior ones; articulating furrow deep, U-shaped, of uniform length (sag. and exsag.), and flexed slightly forward into the apodemes; articulating half ring a little shorter than the remainder of the segment, and flatter in profile. Posterior band of pleurae high, well rounded in section but with the posterior slope slightly steeper than the anterior, maintaining its width well beyond the fulcrum, and then gradually tapering to form a narrow bounding ridge around the end of the pleura; this bounding ridge not present on first segment, slight on second, and fully developed on fourth or fifth segments, this being the consequence of the greater degree of overlap of the more anterior segments during enrollment; anterior band much lower than posterior band and only two-thirds its length (exsag.), with a steep posterior slope and a gentle anterior running on to a narrow flat articulating edge; lateral to fulcrum anterior band facetted; pleural furrow well rounded in section, lateral to fulcrum rapidly diminishing and flexed faintly backward; on reaching facet flexed slightly forward, and then backward again near its tip. Outlines of pleural facets differ with position in thorax; anterior facet with an evenly curved posterior edge, and with a small panderian notch; subsequent segments with progressively straighter posterior edges and sharper curvature on posteroventral edges (pl. 11, fig. 2); size of panderian notch increasing up to segment five, and almost constant thereafter; three to five medium-sized pustules surrounded by about ten smaller ones at ends of rings; crest of rings smooth or with a few small irregular pustules, but anterior slope and posterior slope of articulating half ring with larger numbers of small pustules; posterior band of pleura with sparse small to medium pustules over most of surface, but the lateral extremities with masses of contiguous flattened pustules; anterior band with small to medium pustules

mainly on the posterior slope, but sparse on the anterior slope; pleural facets covered with dense granules. Articulation by large posterior axial process and anterior notch, prominent anterior fulcral process and deep posterior notch, and anterior articulatory shelf between axial furrow and fulcrum which fits beneath the next segment and not into a posterior furrow; first segment with an articulatory shelf extending laterally to the fulcrum, but absent on subsequent segments. Ventral surface with thick apodemes set transversely and thus oblique to the rings (pl. 10, figs. 14, 15); axial doublure covering almost the entire length of the ring medially, but cut away sharply at each side; pleural doublure rapidly expanding in width abaxially from the fulcrum, then maintaining a uniform curve around the pleural tip and projecting up to form a prominent stop at the panderian notch; stops decreasing rapidly in size forward from the fifth segment.

In lateral profile, with base held horizontally. postaxial section of the pygidium standing at 90° to 110°; the crest of the axis only slightly arched and inclined so that the articulating half ring lies slightly behind the anteroventral corners of the pygidium; axial furrow weak posteriorly; a cincture present on the lower part of the pygidium and passing around onto the posterior thoracic segments, marking the position occupied by the edge of the cephalic border roll during enrollment (pl. 9, fig. 9); usually seven complete ring furrows present, but in some specimens the seventh not quite complete; an eighth furrow, not reaching the axial furrow, is convex rather than concave to the rear as are all the others; first ring gently sloping in front, steeply sloping behind or even slightly undercut in some specimens; subsequent rings with less slope as ring furrows tend to fade toward the median line; five, or rarely six, pleurae present, first four clearly defined, but the fifth enlarged and forming the tail piece; first pleural furrow cuts out against the broad facet; subsequent ones definite to the cincture, but only faintly visible beyond it; interpleural grooves distinct and carried down to ventral surface; posterior pleural bands slightly longer (exsag.) than anterior ones, but the fifth segment with an enlarged posterior band passing back to form a protuberant postaxial sector limited on either side by what appear to be expanded extensions of the fifth pleural furrow; border roll evenly curved around to the ventral surface, widest in front and with a pronounced axial notch for the reception of the spine on the hypostome during enrollment; doublure narrow, not forming an angular junction with the border but rather rolled in, and flexed up at its junction with the facets. Ornament of first ring similar to that of thoracic rings, but subsequent ones carrying progressively more pustules, the greatest concentration being on the median parts within the area defined by the apodemes; small to medium-sized pustules much more closely spaced on the inner parts of the pleurae than on the thoracic pleurae; lateral to the cincture pustules of the type found on the cephalic border roll present, and increase in size ventrally; posterior part of axial furrow with fine pustules; doublure smooth.

Perforations widely distributed; pustules on dorsal surface of cephalon each with a main canal almost invariably opening on the posterior slope, except for pustules on the flanks of the various furrows (e. g., pustules on posterior surface of anterior border and posterior surfaces of glabellar lobes with openings on anterior face, and those on flanks of axial furrows with openings in lateral face, pl. 11, fig. 8); in general, smaller pustules have a single perforation, but larger ones sometimes have as many as 7 to 8 smaller perforations arranged in a ring on the flanks, each producing a tiny craterlike eminence on the surface (Shirley, 1936, p. 414; Evitt and Whittington, 1953, p. 53). Similar perforations in pustules on dorsal surface of pygidium and thorax. On cranidium and cheeks inside border furrows internal apertures of major perforations rimmed; on rolled border of cephalon (including rostral plate) and of pygidium, perforations open on steep outer face of pustules; not all these pustules carry perforations, and density of perforations decreases toward doublure; ends of thoracic pleurae densely perforate, with openings lying between the closely spaced pustules; perforations also present in the pustules of the hypostome on the median body, anterior wings, lateral borders, and possibly the posterior border also.

Remarks.—Well-preserved material of this species is abundant, and it has been possible to examine both dorsal and ventral surfaces in some detail. In fact, as much morphological information is available for it as for any described species of the genus. In making comparisons with other species, I have had access to the fine collections in the Museum of Comparative Zoology, Harvard University, which include species from Europe as well as North America. Consequently, it has been possible to compare characters which are not usually considered, but which may be of systematic

value, not only when good material is at hand, but also in comparing fragments. For this reason the comparisons below are unusually detailed.

In many features C. clavicula, new species, is allied to the British group of C. blumenbachi Brongniart and C. lata Shirley from the late Wenlockian and early Ludlovian. However, from C. blumenbachi it can be distinguished by its coarser ornament over the dorsal surface and border roll of the cephalon; deeper occipital furrow; relatively shorter occipital ring; more rounded outline and less steep inclination of the palpebral lobes; more angular lateral border furrow, more angular β in the facial suture; the group of pustules at the end of each thoracic ring rather than a single hump; relatively narrower V-shaped, rather than U-shaped, pleural furrow, which diminishes rapidly in size beyond the fulcrum; the slight marginal cincture on the pygidium; the less pronounced and shorter interpleural furrows on the pygidium; the narrower infolded roll on the pygidium; and the longer posterior border spines and larger spine on the median body of the hypostome.

The holotype of C. lata Shirley has coarse cephalic ornament like that of C. clavicula, new species, and the shape of the glabellar furrow 1p, the anterior outline of the glabella, and the posterior branch of the facial suture are also comparable. However, C. clavicula has a greater length/width ratio of the glabella, no fourth glabellar furrow, and weaker ornament on the thoracic rings. Details of the ventral surface of C. lata have not been published, but, so far as I am aware, no hypostomes with large median nodes are known from the abundant Dudley and Wenlock material, and it seems probable therefore that this feature will prove to be another point of difference.

The closest American species are C. niagarensis Hall, from the Rochester Shale, and C. breviceps Weller, from the Waldron Shale of Indiana. C. celebra Raymond, from the Niagaran dolomites of the Great Lakes area, which in many respects resembles C. breviceps, would not be included in the genus Calymene under Shirley's definition because it lacks a buttress on lobe 2p. Both C. niagarensis and C. breviceps have finer cephalic ornament than C. clavicula. In addition, C. niagarensis has fine densely packed pustules over the thoracic rings and pleurae; weaker marginal furrows on both free and fixed cheeks; a relatively narrower border on the fixed cheeks; more depressed posterior segments on the thoracic pleurae; relatively shorter (exsag.) pleural terminations, with less marked panderian notches; and, on the pygidium, a more pronounced axis, which lies at a lower angle to the plane of the doublure.

C. breviceps has a less tapering glabella; a much shallower preglabellar furrow, which is correlated with a steep uprising in the median anterior margin of the cephalon in general, and deep embayment in the ventral edge of the rostral plate; this in turn is correlated with an emphasized postaxial segment on the pygidium, which fits into the above embayment. The axial furrows lateral to 1p are wider and more pronounced; the occipital furrow is shallower, with a more gentle posterior slope; the posterior marginal furrow is more rounded and the axial ends of the posterior border do not overhang it; the lateral marginal furrows also are shallower and are not angular; the facial suture is curved across the anterior furrow, and is not sharply bent; the thoracic pleural furrows are more pronounced; the thoracic pleural terminations are relatively shorter; both the axial rings and pleurae of the thorax bear fine densely packed pustules; the pygidial crest stands at a lower angle to the plane of the doublure; and finally, the overall shape is more elongate.

Family PHACOPIDAE Hawle and Corda, 1847

Subfamily PHACOPINAE Hawle and Corda, 1847

Remarks.-Within the subfamily Phacopinae (as defined in Harrington and others, 1959) it is possible to isolate a group of genera centered on the genus Phacops, and others on certain Late Devonian genera, for example, Cryphops (Richter and Richter, 1955, p. 60-61). This discussion will not be concerned further with the Late Devonian groups. The Phacops group contains the genera Acernaspis, new genus, Ananaspis, new genus, a new, unnamed genus of Early Devonian age, descendant from Ananaspis, Reedops Richter and Richter, and Phacops Emmrich. The genus Eophacops Delo, commonly included with Phacops, is on a line leading from Acernaspis to the Phacopidellinae, in which group it should be classified. The first appearance of the Phacops group was in the Late Ordovician, and it persisted into the Late Devonian.

Discrimination between the early group mem-

Eophacops	Phacopinae and Phacopidellina: **Acernas pis**
Depressed.	Moderately inflated with evenly curved front; bun-shaped in anterior profile.
Discontinuous, granulose ornament medially.	Discontinuous, granulose ornament medially.
2p weak; 3p strongly impressed laterally, weak axially.	2p weak; 3p weak axially, weak to moderately strong laterally.
Discontinuous anteriorly, not notched laterally.	Continuous, weak anteriorly, notched laterally.
Granulose.	Granulose.
Tranverse or convex backward.	Slightly concave to slightly convex backward.
Unknown.	Unknown.
Granulose.	Granulose.
Smooth or with granules.	Fine granules concentrated on axis and toward pleural tips.
Weak except for first pleural furrow.	Both weak.
	Depressed. Discontinuous, granulose ornament medially. 2p weak; 3p strongly impressed laterally, weak axially. Discontinuous anteriorly, not notched laterally. Granulose. Tranverse or convex backward. Unknown. Granulose. Smooth or with granules.

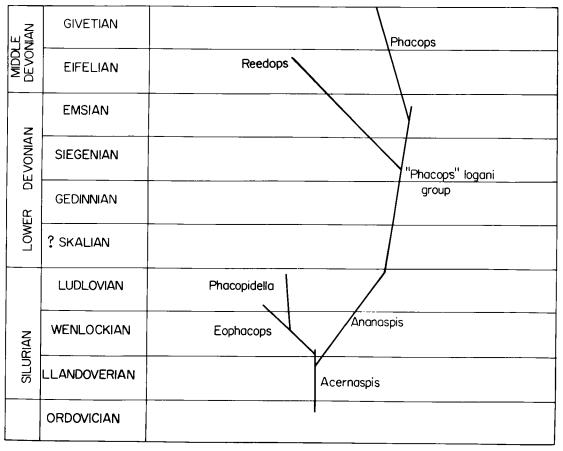
bers, such as "Phacops" elliptifrons (Esmark) and the later ones, such as Phacops latifrons Bronn, is a simple matter, but a more or less continuous variation exists between these end points. The apparent absence of systematically useful breaks is reflected in the suppression by most authors of the genus Portlockia McCoy (Salter, 1864; Richter and Richter, 1923; Whittard, 1938), and by the general absence of attempts to define species groups within the genus Phacops, although mention is made of the existence of such groups by some authors (Richter and Richter 1943, 1955; Öpik, 1953).

In the following discussion an attempt is made to subdivide the group into genera of basically "horizontal" type (Simpson, 1961). Insufficient is known of the evolution of the group to attempt comprehensive definition of independent stocks, and hence a division into "vertical" genera is not yet possible, even if it is desirable. Reedops does appear to represent a short-lived side issue from the main stock and is therefore best considered as a "vertical" genus. In order to make a "horizontal" subdivision, it must be possible to dis-

tinguish morphological characters that change at approximately the same rate throughout the group. In my opinion it is possible to identify such features, the major ones being as follows:

- a. Glabellar ornament which changes from finely granulate in the early forms to tuberculate with superimposed granules, and finally to smooth tubercles.
- b. The proportions of the glabella, the length/width ratios changing from slightly greater than 1:1 in the early forms to approximately 5:6 in the late. Correlated with this is an increase in the angle of divergence of the axial furrows in front of 1p from a range of 25° to 55° in the early forms to one of 65° to 100° in the late.
- c. The outline of the hypostomal suture changes from convex to concave posteriorly.
- d. The change in the ornament of the doublure, which is granulose in early forms, granulose but with the granules elongated and arranged in rows in some Early Devonian species, and formed predominantly of linear ridges in Middle Devonian species (some evidence suggests a similar change

Ananas pis	Reedops	Phacops
Moderately inflated with steep front; bun-shaped in anterior profile.	Inflated, overhanging border in front.	Usually inflated with vertical front; squarish in anterior profile.
Discontinuous, normal glabellar orna- ment medially.	Continuous, not interrupted by ornament medially.	Continuous, not interrupted by ornament medially.
2p moderately to strongly impressed; 3p not more strongly developed laterally.	Absent or weakly impressed.	Absent or weakly impressed.
Discontinuous or very weakly continuous anteriorly; notched laterally.	Notched laterally, absent or weak anteriorly.	Notched laterally, continous, deep anteriorly.
Granulose.	Granulose, but with granules elongate and arranged linearly.	Terrace lines, passing into elongate granules in places.
Transverse to slightly convex backward.	Transverse to slightly convex backward.	Concave backward.
Short posterior border; ornament of granules; strongly tapered.	Short or long posterior border, not strongly tapered, low anterior wings.	Long posterior border; ornament of terrace lines and elongate granules; strongly tapered.
Small tubercles with superimposed granules.	Very small tubercles (pustules), without granules superimposed; often partly smooth.	Coarse tubercles on top becoming finer and often linear in front.
Thorax with granulose tubercles on axis; pygidium with granular axis.	As for glabella.	Almost smooth to coarsely tuberculate without granules.
Both moderate to strong.	Both weak.	Weak interpleural and strong pleura furrows.



Text-figure 6. Evolutionary relationships of certain members of the Phacopinae and Phacopidellinae.

in the ornament of the hypostome, but this cannot yet be adequately documented).

- e. The gradual strengthening of the median part of furrow 1p (the intercalary furrow).
- f. The change from granulation to tuberculation on both thorax and pygidium.

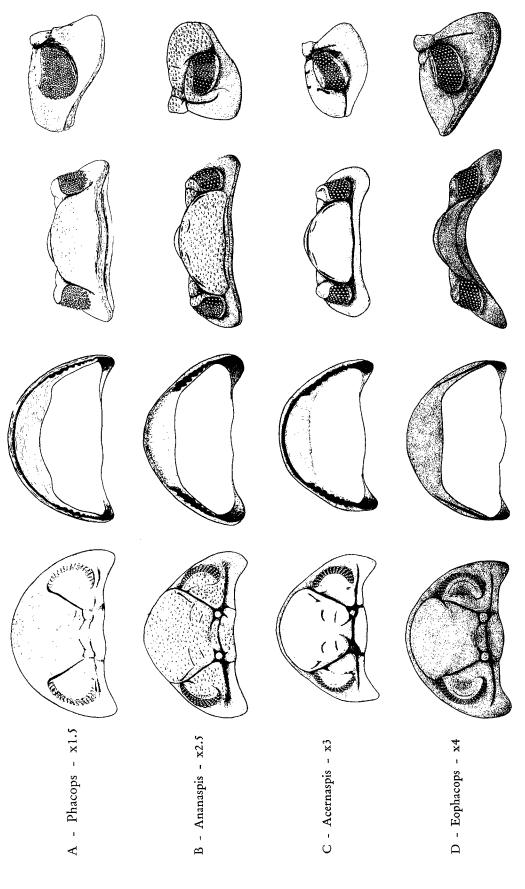
In addition to these "sequential" morphological characters, there are others that appear and then disappear, and some of these subsequently reappear. For example, the vincular furrow is continuous and moderately strong in the members of the genus Acernaspis in the Llandoverian and Wenlockian, it is weak or absent around the frontal region in the predominantly Wenlockian and Ludlovian Ananaspis, but reappears in the Early Devonian species of Ananas pis type such as "Phacops" raymondi and in the genus Phacops. The peculiar depression of the glabella and the development of the nonnotched vincular furrow characteristic of Eophacops appear to have evolved only once, and persisted on into the genus Phacopidella, which is usually considered to be in a separate subfamily

(Struve in Harrington and others, 1959). Eye size and shape show no systematic changes with time. This is of interest in view of the taxonomic importance of eye changes in the Late Devonian genera descendant from *Phacops*.

A summary of the characters considered pertinent for the diagnosis of the genera discussed herein is presented in table 4.

It is improbable that all the "sequential" characters will change at the same rates in all stocks in all areas. Yet on a broad scale it is possible to define genera by their position on the evolutionary scale, that is, by the occurrence of certain character combinations and, in addition, by the appearance of various "nonsequential" characters. This procedure has been followed below even though it is realized that, because of variable evolutionary rates, some species will not fall neatly into the groups as defined. Examples of this are given in the remarks on the various genera discussed.

In undertaking this work I have examined the primary types or topotypes of several European, American, and Australian Silurian-Middle Devon-



Text-figure 7. Dorsal, ventral, anterior, and lateral aspects of the cephala of the genera Phacops, Ananaspis, Acernaspis, and Eophacops. The reconstructions are based upon Phacops rana milleri Stewart, Ananaspis guttulus, new species, Acernaspis orestes (Billings), and Eophacops trapezionstructions are based upon Phacops rana milleri Stewart, Ananaspis (Barrande).

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ian species of phacopids. Details are given below:

Primary types examined

Acernaspis? marklandensis (McLearn, 1918)
Eophacops matheri Delo, 1940
Eophacops cerviculata Ulrich and Delo, 1940
Eophacops mancus (Foerste, 1919)
Eophacops? pulchellus (Foerste, 1885)
Ananaspis? budsonicus (Hall, 1861)
Ananaspis typhlagogus (Öpik, 1953)

Primary types and topotypes examined

Acernaspis elliptifrons (Esmark, 1833)
Acernaspis orestes (Billings, 1860)
Acernaspis macdonaldi (Fletcher, 1948)
Eophacops handwerki (Weller, 1907)
Ananaspis? crosslei (Etheridge and Mitchell, 1896)
Ananaspis guttulus Campbell, new species
Ananaspis? raymondi (Delo, 1935)

Topotypes or probable topotypes examined

Eophacops musheni (Salter, 1864)
Eophacops trapeziceps (Barrande, 1846)
Ananaspis communis (Barrande, 1852)
Ananaspis stokesi (Milne-Edwards, 1840)
Phacops latifrons (Bronn, 1825)
Phacops schlotheimi (Bronn, 1825)
Phacops breviceps Barrande, 1846
Phacops degener Barrande, 1852
Phacops major Barrande, 1852
Phacops rana Green, 1832
Phacops rana milleri Stewart, 1927
Reedops bronni (Barrande, 1846)
Reedops sternbergi (Hawle and Corda, 1847)
Reedops cephalotes (Hawle and Corda, 1847)

Genus Acernaspis, new genus

Type species.—Phacops orestes Billings, from the Jupiter and Gun River Formations (Llandoverian) of Anticosti Island.

Diagnosis.—Small for the subfamily; glabella only moderately convex in longitudinal profile, never with a vertical front wall, nor overhanging the anterior margin; length/width ratios of glabella 1 or greater; furrow 1p not continuous, but with its inner end directed strongly forward; 2p and 3p moderately impressed, 3p, but not 2p, being connected to the axial furrow; strong incision into the occipital ring at the inner end of the occipital apodeme; axial furrow strong and straight on the flank of the glabella; preglabellar furrow weak; facial sutures continuous around anterior of cephalon and cutting across anterolateral corners of glabella; eyes large; genal angle subrounded to pointed; dorsal surface covered with minute granules; anterior doublure long, and granulate, the granules not arranged in rows; vincular furrow continuous, moderately strong anteriorly, and notched laterally to receive the ends of the

thoracic pleurae. Thoracic ring with an incision near the outer end, but without a lateral node. Pygidium with six to eight rings, the posterior ones being poorly defined, and five or six pleurae; all pygidial furrows narrow and rather weak; thorax and pygidium either smooth or with minute granules.

Remarks.-McLearn (1918, 1924) used the generic name Portlockia McCoy to cover species of the Phacops orestes type. The first formal designation of a type species was apparently that of McLearn (1918, p. 35), who designated Calymene stokesi Milne-Edwards. C. stokesi was not among those listed by McCoy as species of his genus Portlockia; however, McLearn, in choosing it as type species, indicated that Portlockia sublaevis McCoy (one of the original species) was a subjective synonym of C. stokesi. Under the Règles (Art. 69, a, iv) this would make C. stokesi the type if the synonymy were upheld; however, if it were not upheld, presumably P. sublaevis would become the type. The evidence seems insufficient to suggest that these two species are conspecific, despite the fact that Salter (who saw the original of P. sublaevis) said that they are (Salter, 1864, p. 22). On the other hand, McCoy's explicit statements that the cephalon has such fine granules that it appears smooth to the naked eye and that the eyes are small certainly suggest that they are not conspecific.

Whittard indicated that he was unable to locate the types of P. sublaevis; and, although some of McCoy's types have been found in the National Museum of Ireland, Dublin, Dr. J. S. Jackson informs me that P. sublaevis is not among them. Further, I have been unable to obtain topotypic material of the species; as Delo and others, have stated, the species cannot be interpreted on the figures and description of McCoy. It is still possible, from the little that is known of the species, that it is congeneric with Phacops orestes, but I consider the possibility to be remote. I have therefore erected the genus Acernaspis with P. orestes Billings as type, a species which is well known morphologically and stratigraphically, and which occurs abundantly. I have based my interpretation upon the specimens YPM 24885-8, the two specimens figured by Delo (1940) now labeled YPM 11313 and YPM 24889, and the type material.

Species included in this new genus, in addition to the type species, are "Phacops" elliptifrons (Esmark), from the Llandoverian of Norway, Estonia, and Great Britain; and Phacops macdonaldi Fletcher, from the Llandoverian of New South

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Wales. It is probable that Phacops primaevus Clarke, from Zone F4 (Ordovician) of Gaspé, and Phacops (Portlockia) marklandensis McLearn, from the Ross Brook Formation of Arisaig, Nova Scotia, belong here. The type material of the latter is not sufficiently well preserved to allow a definite decision to be made. The holotype has been cleaned enough, however, to demonstrate that the dorsal cephalic ornament, the ornament of the cephalic doublure, the shape of the axial furrows, the lateral glabellar profile, the presence of a vincular furrow, and the furrows on the pygidium are all consistent with an assignment to Acernas pis. In fact, I see no reason why the species should not be synomymized with Acernaspis orestes. Delo (1940, p. 28) placed it in Eophacops.

Maksimova (1962) recently described three species of the genus, from the Upper Ordovician and Llandoverian of the Siberian platform, as members of Eophacops. The representatives of E. nanus Maksimova and E. pulcher Maksimova, figured on her plate 11, appear to be normal members of Acernas pis. Those figured as E. quadrilineatus (Angelin) in figures 11, 12, and 14 of plate 10, also appear to belong to Acernas pis, although it is difficult to be certain of this (the specimen in figs. 13a,b could be a true Eophacops).

Genus Reedops Richter and Richter, 1925

Type species.—Phacops bronni Barrande, from the Lower Devonian of Czechoslovakia.

Diagnosis.—Medium size for the subfamily; glabella inflated, produced anteriorly, and markedly overhanging the anterior border; length/width ratios of glabella range from 1:1 to 1:1.15; angle of divergence of axial furrows on cephalon 60° to 85°; furrow 1p deep, transverse, and continuous; furrows 2p and 3p not impressed, and distinguishable mainly by dark lines in the exoskeleton; preglabellar furrow weak to absent; eyes small to moderate in size, and situated well forward; ornament of cephalon of scattered granules or fine pustules, usually densest on the borders and the anterior part of the glabella, and becoming more scattered toward the occipital region; anterior doublure convex in lateral profile, and ornamented with transversely elongated granules; vincular furrow absent in front, narrow, and slightly notched laterally*; hypostomal suture convex backward; hypostome less strongly tapering

than that of *Phacops*. Thoracic segments with well-differentiated nodes on each side of axis; pleural furrows deep. Pygidium with pleural furrows rapidly weakening from front to back, and interpleural furrows almost indistinguishable; ornament of thorax and pygidium composed of granules or pustules like those of the cephalon, most crowded on the axis and the lateral parts of the pleurae, and sparse on the adaxial parts of the pleurae.

Remarks.—Reedops apparently represents a side branch from the main Phacops-group stock. It was probably derived from Ananaspis and became extinct without further issue. The oldest species are said to be Silurian (Wedekind, 1911; Delo 1940), but I have been unable to confirm any such occurrences. In any case, the genus did not become abundant until the Early Devonian, and it apparently disappeared in the Eifelian.

Genus Phacops Emmrich, 1839

Type species.—Calymene latifrons Bronn, from the Eifelian of the Rhine Valley.

Diagnosis.—Exoskeleton of medium to large size for the subfamily; glabella inflated, tending to be flattened on top, with an almost vertical front wall, rapidly expanding to the front, and with length/width ratio ca. 5:6; furrow 1p continuous across the glabellar stalk; furrows 2p and 3p weakly impressed and partly or completely obscured by the tuberculation; no incision in the occipital ring behind the inner edge of the occipital apodeme; large tubercles on top of the glabella gradually diminishing in size toward the preglabellar furrow, and becoming progressively

Alberti gives the range of the genus as Praguian to

^{*} Since this bulletin went to press I have received a copy of an article by Alberti (1965), in which he recorded the presence of a shallow vincular furrow around the anterior margin of the cephalon of certain specimens of Reedops bronni. For this reason he regarded the character of the vincular furrow as of doubtful taxonomic significance. It should be pointed out, however, that a shallow furrow of the type Alberti recorded is probably indicative only of the shape of the pygidial doublure and its position against the ventral side of the cephalon when the animal was enrolled. That is, the posterior end of the pygidium still overlapped the anterior end of the cephalon, as is normal for Reedops. A similar condition exists in Ananaspis. On the other hand, in both Phacops and Acernaspis the whole edge of the pygidium fitted into the vincular notch on the cephalon without overlapping, and thus produced a different type of closure. I therefore still consider the character of the vincular furrow to be of taxonomic value.

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more transverse in some species; no fine granulation over the glabellar tubercles; preglabellar furrow definite but faint; borders of free cheeks with few to many scattered tubercles much weaker than those of the glabella, and with some shallow pits particularly towards the genal region; eyes large, high, close up to the axial furrow in front and the posterior border furrow behind; cephalic margins followed by slight ridges forming a braided pattern; vincular furrow entire, with multiple notches for thoracic pleural tips laterally, and smooth or with a very fine granulation below the glabella; stop for first two thoracic segments close to the rear margin; anterior part of doublure with wavy linear ornament subparallel to the margin but on the median posterior part breaking down into discrete transverse fragments arranged in rows; these linear ridges with sharp anterior and gentle posterior slopes; hypostomal suture markedly concave. Hypostome extending back beyond the rear edge of the dorsal surface of the cephalon, produced posteriorly into a short median marginal spine flanked by a pair of smaller spines; posterior border long; posterior border furrow wide and strong, and supplementary furrow weaker; hypostomal ornament with a marginal "braid," and linear ridges on the body similar to those of the doublure arranged concave forward, the degree of concavity increasing toward the posterior; ridges break down into discrete elements behind the median furrow and on the anterior wings. Thoracic rings without incisions near the axial furrow and without lateral nodes. Pygidium with nine to eleven rings and up to eight pleurae, the most posterior ones being weakly defined; border of pygidium not separated off by a furrow, and without traces of pleural or interpleural furrows; interpleural furrows on inner parts weak to indistinguishable; rings and pleurae of both thorax and pygidium with weak to strongly developed tubercles; doublure of pygidium with concentric terrace lines.

Remarks.—The above diagnosis is more restrictive than that commonly used (Delo, 1935a, 1940; Whittard, 1938; Stumm, 1953; Richter, Richter, and Struve in Harrington and others, 1959). In addition to the type species, it inclues P. fecundus major Barrande, from the Eifelian of Czechoslovakia; P. schlotheimi (Bronn), from the Eifelian of Germany; and probably P. accipitrinus accipitrinus (Phillips), from the Upper Devonian of Great Britain and Belgium; P. granulatus Muenster, from the Upper Devonian of Germany; P. latifrons grzegorzowi-

censis Kielan, from the Eifelian, P. sobolewi Kielan and P. schlotheimi skalensis Kielan, from the Givetian of Poland (Kielan, 1954); P. altaicus Chernyshev, from the Eifelian of Russia; P. rana Green and its numerous subspecies, from the Eifelian and Givetian, and P. iowensis Delo from the Givetian of North America (for summary, see Stumm, 1953); P. papulatus Richter and Richter, from the Eifelian, P. erfoudensis Richter and Richter and P. accipitrinus accipitrinus (Phillips), from the Upper Devonian of Morocco (Richter and Richter, 1943). The list is not intended to be exhaustive.

Thus most members of the genus are either Middle or Late Devonian in age. However, if multiple character diagnoses of the type given above are used, it is only to be expected that, since evolution commonly proceeds on a mosaic pattern and at different rates in different stocks, there may be many species that satisfy the diagnosis only partially. This situation is illustrated by the occurrence in the late Early Devonian of species which are obviously close to the typical Phacops but which are "primitive" in one or more characters. An example is P. fecundus degener Barrande, which, according to Chulpáč (1957, 1962), first appears in the Emsian and persists into the Eifelian. It is "primitive" in its glabellar profiles, shape of the posterior border furrows, and mainly elongate granules rather than ridges in the cephalic doublure. In all these features it resembles Early Devonian species of the Ananaspis type, for example, "Phacops" raymondi Delo (see below). It appears to be a true intermediate between such species and Phacops. P. breviceps Barrande, which, according to Chulpáč (1962), is restricted to the late Eifelian Acanthopyge limestone, is probably an offshoot from the P. fecundus degener stock, and has developed all the typical characters of Phacops sensu stricto, apart from the squarish glabellar profiles.

Other examples of this sort are probably to be found in regions where there is a good phacopid succession, for example, in North Africa, whence Le Maître (1944, 1952) has described and recorded many species. Unfortunately, details of the dorsal ornament and of the ventral structures are wanting for most species, and consequently accurate assignment to genera is not possible at present.

The genus encompasses a considerable range of morphological types, but no clearly defined trends have yet been discovered. In particular, variability has been noted in the following characters. Some species have large tubercles of rather uniform size ANANASPIS 35

on the top of the glabella and others have a variety of sizes, whereas on the front of the glabella they range from small equidimensional tubercles to small flat transverse ridges. Furrows 2p and 3p are usually distinguishable, if not as faint furrows then as somewhat darker colored lines in the shell. However, they are never deeply impressed, and their courses are irregular as a result of interference from the tubercles. The axial furrows fade at the anterolateral corners of the glabella in some species, and, where this occurs, the glabella expands outward in front of the eyes. The anterior profile of the crest of the glabella ranges from almost flat to gently rounded. The strength of the tuberculation on the cephalic borders and on the thorax and pygidium ranges from very coarse and strong to coarse and almost imperceptible.

Genus Ananaspis, new genus

Type species. — Phacops fecundus communis Barrande, from the Kopanina beds (Ludlovian) of Czechoslovakia.

Diagnosis.—Exoskeleton of small to medium size for the subfamily; glabella inflated, domed in both lateral and anterior profiles, rapidly expanding forward, and with a length/width ratio of approximately 1:1; furrow 1p not continuous across the glabella but interrupted medially by tubercles; furrows 2p and 3p distinctly impressed; a distinct incision present in the occipital ring behind the inner end of the occipital apodeme; tubercles of various sizes over the glabella in front of the occipital ring, showing no tendency to diminish in size toward the front; occipital ring with a single median tubercle flanked by much weaker irregular tubercles; tubercles also present on inner parts of fixed cheeks; dorsal surface of cephalon (including surface of tubercles) covered with fine granules; posterior border furrow short (exsag.), extending laterally beyond the eyes and then bent sharply forward; axial furrows deeply depressed on the upper surface, and sharply defining the anterolateral corners of the glabella; preglabellar furrow distinct; eyes close to the axial furrows in front, but well separated from the posterior border furrow behind; cephalic margins with a granulose ornament; vincular furrow with multiple notches laterally, weak or absent anteriorly; stop for first thoracic segment well forward; doublure and (where present) anterior part of vincular furrow with granulose ornament; hypostomal suture transverse or slightly convex backward. Hypostome with three small spines at the posterior end; central body more convex longitudinally than in *Phacops*; maculae small, forward of the midlength of hypostome; short posterior border, with a weak posterior border furrow and a more pronounced supplementary furrow; surface ornament apparently granulose—not of terrace lines. Thoracic rings with anterior incisions separating off lateral nodes. Pygidium with eight to ten rings and six to eight pleurae; border of pygidium smooth and not separated off by a furrow; interpleural furrows well developed. Axis of thorax and pygidium with very weak granulated tubercles or with granules only, and pleurae with few scattered granules.

Remarks.—Ananaspis communis (Barrande) has been chosen as type species because it is well known, has been long established, and is abundant. Ananaspis guttulus, new species, on the other hand, is known from relatively few individuals, many of which are incomplete or worn. In addition to these two species, Phacops stokesi (Milne-Edwards), from the Wenlockian of Great Britain (Salter, 1864) is included. P. crosslei Etheridge and Mitchell, and P. serratus Foerste, from the Ludlovian of southeastern Australia (Etheridge and Mitchell, 1896), are only doubtfully included, as they exhibit some features in common with the Early Devonian species alluded to below.

Possibly the genus evolved as early as late Llandovery, although at this stratigraphic level only one possible species is known, namely *Phacops typhlagogus* Öpik, 1953, from the "Illaenus band" in Victoria, Australia. The type specimens of *P. typhlagogus* have been partly destroyed by fire and no surface details remain. However, the internal mold shows that the glabella was tuberculate and that the anterior margin of the cephalic doublure was beveled in a manner similar to that of species of *Ananaspis*. In Europe and North America the genus appears first in the Wenlockian and persists into the Ludlovian.

Several Early Devonian species (e. g., "P." logani Hall, P. raymondi Delo) are closely related to members of this genus, but have a deep continuous vincular furrow. Upon the basis of the definition of Ananaspis, given above, they would thus be excluded. They are much nearer to this genus than to Phacops sensu stricto, and for this reason they are listed above as Ananaspis?. However, when they are described in more detail, it will probably be necessary to establish a new genus to contain them.

Ananaspis guttulus, new species

Pl. 3, figs. 5, 6; pl. 14, figs. 1-15

Types.—Holotype OU 5626 and paratypes OU 5636, OU 5636A, OU 5637, OU 5647, and OU 5648, from SE1/4 SW1/4 sec. 4, T. 2 N., R. 6 E. (Amsden collection locality P6); paratypes OU 5627 and OU 5634, from NW1/4 SW1/4 sec. 4, T. 2 N., R. 6 E.; paratype OU 5635, from NE1/4 sec. 29, T. 3 N., R. 6 E.; all Pontotoc County. Paratypes OU 5629 and OU 5631 from SE1/4 sec. 30, T. 2 S., R. 1 E., Carter County (Amsden measured section Ca1, bed Q).

Description.—Glabella rapidly expanding; maximum width at anterior border furrow and minimum width at lobe 1p; ratio of maximum/ minimum widths 2:1; width at occipital ring only slightly greater than minimum width; glabellar width about three-fifths of width of cephalon; in lateral profile a sharp drop from the occipital ring to lobe 1p, a slight rise on to the anterior part of the glabella, and an almost vertical anterior margin; in some specimens glabella not quite reaching the margin and in others a slight overhang is present; axial furrow very broad and shallow at the occipital ring, increasing slightly in depth at the occipital furrow and then running an almost-horizontal course to the anterior edge of the eye and dropping steeply to the border furrow; preglabellar furrow narrow and shallow; occipital ring of normal shape for a phacopid, but sharply cut into by furrows at the inner ends of the apodemes; central part of ring 1.5 times as long (sag.) as lateral parts (exsag.); furrows 1p deep and transverse laterally (up to 1 mm in from axial furrow in adults), but with their shallow inner portions directed forward at 25° to 30° to a transverse line; connecting furrow faintly developed in some specimens, absent in others; an almost circular node cut off at each end of ring 1p by shallow, but definite, furrows; furrows 2p faintly impressed, straight, to slightly curved, subparallel to the inner parts of 1p, and never reaching the axial furrow; furrows 3p even more lightly impressed and consisting of a comma-shaped inner part, and a straighter outer part which runs forward to meet the axial furrow just behind the anterior edge of the palpebral lobe; measured along the outer edges of the transverse parts of the furrows (where they are farthest apart), ratio of length of lobe 2p to length of lobe 3p is ca. 3:4. Posterior border furrows short (exsag.), shallow, with an almost symmetrical U- to slightly Vshaped section, almost straight, and inclined back-

ward at ca. 10° to a transverse line; tips of furrows curving forward and fading away inside genal angle; posterior border tapering slightly from the axis to the fulcrum, and then broadening to about twice this length (exsag.) behind the outer limits of the eyes. Palpebral lobes broad, and with their widest parts in line with the inner tips of furrows 2p; outline comma-shaped with the greatest curvature to the rear; shallow furrows cross the lobes, pass around the rear of the visual surface of the eye and then below it, where they form the lateral border furrows; palpebral lobes never as high as the glabella; eye variable, made up of 60 to 120 lenses (see remarks); eye surface not vertical, but in anterior profile sloping at ca. 70° to the horizontal. Facial suture not distinguishable in front of eyes; posterior branch of suture arcing forward slightly from the rear of the eye, and then back to meet the margin slightly behind the line of the posterior border furrow; on the doublure, suture curving back slightly from the margin, and then forward to meet the inner edge a short distance behind the end of the vincular furrow.

Anterior doublure (sag.) 0.34 to 0.42 the total length of the cephalon; in vertical ventral view broad central part of hypostomal suture straight or slightly convex posteriorly; lateral to this, at the dorsad deflection of the doublure, a slight bulge present; dorsad deflection ca. 1 mm inside the axial furrow; in posterior view central part of hypostomal suture gently arched; in lateral profile anterior part of doublure slightly convex in front and slightly concave behind; lateral, dorsally deflected part low, (max. height 1 mm) and continued back to a point opposite the rear end of the eyes, there terminating abruptly to form the stop for the first thoracic segment during enrolling; vincular furrow present laterally, reaching as far forward as the straight hypostomal suture, with its inner edge slightly and progressively more dorsad posteriorly than its outer edge, and containing about eight notches for the reception of the thoracic pleural tips; posteriorly the doublure swings around in a broad arc and wedges out at the fulcrum; on some specimens a faint continuation of the vincular furrow present around the anterior of the shell immediately inside the margin. Hypostome unknown.

Ornament of glabella of small tubercles and granules; granules most closely spaced on the anterior lobe, being both on and between the tubercles; more posteriorly, granules restricted to the tubercles and to the nontuberculate areas of

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lobes 1p, 2p, and 3p, close to the axial furrows; occipital ring with less distinct tubercles than elsewhere on the glabella, and with granules on and between the tubercles; fixed cheeks inside palpebral furrow with similar ornament to occipital ring; lateral and anterior borders with closely spaced granules; posterior border smooth except near genal angles, there becoming granulate; furrows smooth.

Thorax with moderately arched rings; in dorsal view ends of rings swing slightly forward, and separated from the front of the ring by a deep incision, and by a much shallower one from the rear, lying lateral to the anterior one; rear incision does not break the smooth posterior outline of the ring (see rings of Acernaspis orestes, pl. 13, fig. 7); no true lateral nodes developed; articulating furrow shallow, and articulating half ring approximately equal in length to remainder of ring; axial furrows shallow; pleural furrow straight in dorsal view and not extending onto the pleural facet; fulcrum prominent; posterior band well rounded and bearing a sharp articulatory flange posteriorly between the fulcrum and the axial furrow; lateral to fulcrum, surface of posterior band beveled off; anterior band well rounded; facet with arcuate anterior and posterior edges, and with the anteroventral tip angular; ornament on rings of weak to very weak tubercles covered with granules: pleurae smooth or with sparse very fine granules on the posterior band, particularly behind the

Pygidium with 8 + 1 rings (eight visible on most specimens, the extra one only on particularly well-preserved ones), and seven pleural furrows (best preserved specimen shows slight indentations on the backs of first five rings); facets deep, extending into the fulcra and back as far as the fourth axial ring; pleural furrows shallow, first two pairs gently curved backward, subsequent ones straight, and all fade away above the inner edge of the doublure, leaving a broad smooth border; interpleural furrows weak, and only five pairs visible; ornament confined to the crests of the rings and consisting of fine granules only, or of granules on the faintest of tubercles; doublure very wide, with a broad outer band gently inclined to the horizontal and an inner, more steeply inclined band.

Remarks.—Ananaspis guttulus exhibits a wide variation in the size of the eyes. On the one hand, some individuals have a maximum of five lenses in any vertical row, and, on the other, some have seven. The number is not a function of size; two

specimens of about the same size (OU 5636, OU 5648) have the maximum and minimum number, respectively. Lens size on the other hand does appear to vary with the size of the specimen. The specimens with the fewer lenses have palpebral lobes which stand as high as those of the other types, but they have a higher subocular furrow. From the specimens available at present, this character does not seem to be a dimorphic one, but a larger sample is desirable.

Ananaspis guttulus is smaller than Ananaspis communis (Barrande), has finer tubercles on the glabella, less strongly curved glabellar furrows 2p and 3p, the posterior edge of the eyes further back, less angular genae, and stronger pleural furrows on the pygidium. A. stokesi (Milne-Edwards) from the upper Wenlockian and Ludlovian of Great Britain is the most closely related species yet described. The main differences are details of proportion—the axis of the thorax and the pygidium is relatively broader, and the pleural and interpleural furrows of the pygidium are stronger in A. guttulus than in A. stokesi. Minor differences in ornamentation may also exist, particularly in the distribution of small tubercles on the thoracic axis, but the material of A. stokesi I have examined is not well enough preserved to confirm this.

No comparable species have been described from North America.

Subfamily PHACOPIDELLINAE Delo, 1935

Genus Eophacops Delo, 1935

Type species.—Phacops handwerki Weller, from the Niagaran dolomites at the Chicago Drainage Canal, Lemont, Illinois (probably late Wenlockian, but possibly early Ludlovian).

Diagnosis.—Small for the subfamily; glabella depressed, with only gently arched lateral and anterior profiles, only gradually expanding to the front, and with length/width ratios of ca. 1:1; furrow 1p not continuous, median part bearing the normal glabellar ornamentation; 2p weakly impressed; 3p strong at the axial furrows, weakening axially, and with the transverse part almost indistinguishable; eyes large, close to axial furrow in front and the posterior border behind; no tubercles anywhere on the cephalon; surface with fine granules rather closely spaced on the glabella, and more widely spaced on the cheeks; vincular furrow present, laterally without notches for the thoracic pleural tips, and weak to absent anteri-

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orly; ornament of doublure granulose; hypostomal suture transverse to convex backward; hypostome unknown. Thoracic pleurae with narrow inner parts and long (tr.) steeply downturned outer parts. Pygidium with six to eight rings and four to six pleurae; all pygidial furrows weakly impressed. No tubercles on either thorax or pygidium; scattered granules present.

Remarks. — In erecting Eophacops, Delo (1935a) commented on the unsatisfactory position with regard to our knowledge of the type species of Portlockia, P. sublaevis McCoy, and it was his intention that Eophacops should be a substitute for Portlockia as it had been interpreted by McLearn (1918, 1924).

In addition to the type species, this genus includes *E. matheri* Delo, from the Niagaran of Indiana; *E. mancus* (Foerste), from the Cedarville Dolomite (Wenlockian) of Indiana; *E. trapeziceps* (Barrande), from the Liteň and Kopanina beds (Wenlockian-Ludlovian) of Czechoslovakia; and *E. musheni* (Salter), from the Wenlockian of England. A species possibly referable to the genus is *Phacops pulchellus* Foerste, from the Clinton Group, Dayton, Ohio (Wenlockian).

The type species is not well understood. By courtesy of Dr. Eugene Richardson of the Chicago Natural History Museum I have been able to examine Weller's cotypes. They are internal molds in crystalline dolomite, and it is possible to determine only gross structure from them. It is clear, however, that no part of the exoskeleton was tuberculate. No surface details are known for E. matheri Delo, or for E. mancus (Foerste). However, E. trapeziceps (Barrande) and E. musheni (Salter) both have a fine granulation on the cephalon, and possibly on the thorax and pygidium as well.

I have included Phacops trapeziceps Barrande in this genus rather than in Phacopidella Reed, as has been done by certain Czech authors (Horný, Prantl, and Vaněk, 1957). The reasons for this course are as follows: specimens in the MCZ and YPM collections do not show the glabellar furrows joining medially as in the type species of Phacopidella, P. glockeri; the thorax is proportionately narrower (length of axis/width of thorax ratios ca. 1:1 for E. handwerki and P. trapezice bs, and ca. 5:6 for P. glockeri), more tapering, and more strongly turned down beyond the fulcra; and the pygidium has a relatively narrower axis, more axial rings, and more pleurae. These differences between the pygidia are not size dependent, as comparisons have been made between specimens

of comparable size. In all these features *P. trapeziceps* is close to *Eophacops handwerki*. Similar comments apply also to *P. musheni* (Salter). (It is noted that the inclusion of *P. trapeziceps* in *Eophacops* raises no problem about the synonomy of *Eophacops* and *Glockeria* Wedekind. Reed [1927, p. 313] suggested that the status of *Glockeria* would have to be reviewed if *P. trapeziceps* were found to be generically distinct from *P. glockeri*, but this would be an invalid procedure.)

It is worth emphasizing, however, that Eophacops is more closely related to Phacopidella than to its nearest relative in the Phacops group. The most striking features shared by Eophacops and Phacopidella, but absent from most species of Acernas pis, are the more depresesd glabellar profiles, the strong junction between furrows 3p and the axial furrows, the shallowing and flexing of the axial furrows near the anterior end of the palpebral lobes, and the incomplete vincular furrow which lacks notches for the thoracic pleural tips. On the other hand, features that Eophacops has in common with Acernas pis, but not with Phacopidella, are the relatively larger and more posteriorly placed eyes, the failure of furrows 1p, 2p, and 3p to join longitudinally at their axial ends, facial sutures continuous around the front of the glabella, the narrower thorax with sharply downturned pleural ends, and narrower pygidium with much weaker and fewer ring, pleural, and interpleural furrows. Further, at least one species of Acernaspis, A. elliptifrons (Esmark), has strong glabellar furrows 3p rather like those of Eophacops.

For what it is worth in our present state of ignorance, it is noted that the oldest *Eophacops* appears earlier in the Wenlockian than does *Phacopidella*, and the two coexist into the Ludlovian. Both morphological and stratigraphical evidence supports the evolutionary scheme outlined above.

Destombes (1964, p. 50) presented an alternative view of the derivation of *Phacopidella*. He traced its development from *Kloucekia* to *Pre-phacopidella* (an Ashgillian form from Morocco), and thence to *Phacopidella*. The structure of glabellar lobes 1p and 2p and the shape and segmentation of the pygidium of *Phacopidella* suggest affinities with the Phacopinae rather than either the Acastinae or the Zeliszkellinae, to which *Kloucekia* (and *Prephacopidella*) are currently assigned (Struve in Harrington and others, 1959; Whittington, 1962).

Maksimova (1962, p. 85-87), basing her interpretation of the genus upon certain Russian spe-

cies, has indicated that it has a notched vincular furrow, but, as shown above, these species should be placed in *Acernaspis*.

Family DALMANITIDAE Vogdes, 1890

Genus Dalmanites Barrande, 1852

Type species. — Trilobus caudatus Brünnich, from the Wenlockian of Coalbrookdale, England.

Range.—Silurian-Lower Devonian; cosmopolitan.

Dalmanites rutellum, new species

Pl. 16, figs. 1-13; pl. 17, figs. 1-13; pl. 18, figs. 1-4

Types.—Holotype OU 5624, from SE 1/4 sec. 5, T. 2 N., R. 6 E., Pontotoc County. The paratypes, all from the adjacent sec. 4, T. 2 N., R. 6 E., are as follows: OU 3630 and OU 3632, from NE 1/4 SW 1/4 SE 1/4; OU 4960A-B, from near center of section; OU 4966A-F and OU 5623A-D, from C SW 1/4 SE 1/4; and OU 5625, from SE 1/4 SW 1/4.

Other material.—Three enrolled specimens, YPM 24882-4, with cephalon, pygidium, and at least part of thorax, from NE \(^1\)/4 sec. 9; many other specimens, particularly pygidia, from the paratype localities; and others from NW \(^1\)/4 SW \(^1\)/4 sec. 5; all in T. 2 N., R. 6 E., Pontotoc County. Other specimens from 0.25 mile southeast of Rayford quarry, SE \(^1\)/4 NE \(^1\)/4 sec. 28, T. 1 S., R. 2 E., Murray County.

Description. — Cephalon exclusive of genal spines, twice as wide as long, and inclusive of genal spines, as wide as long; in outline, flanks along the spines tend to be straight, and the remainder almost semicircular, broken only by a slight, well-rounded anterior protuberance; posterior margin almost straight between the fulcra, then bent back at an angle of ca. 20° toward the genal spine where the angle increases rapidly; glabella widest in front of the midpoint of the anterior lobe, and narrowest at the occipital furrow; ratio of minimum width/maximum width of glabella ca. 3:5; length/width 12:10 to 13:10; axial furrows deepest at the occipital furrow, rise gradually and become shallowest just behind midlength of lobe 3p, then fall and become slightly deeper (though still broad and shallow) around the anterior lobe; lateral border furrows broad and shallow, rapidly fading away in front of the genal spines; posterior border furrows narrow behind the eyes, broadening rapidly lateral to the midpoint of the eyes, and tapering to a point slightly behind and above the ends of the lateral border furrows, in such a way as to give a lanceolate outline to the furrow; anterior and lateral borders sloping gently down and out to the sharply inflected doublure, and fade away gradually along the genal spine; posterior border between the axial furrow and directly behind the midpoint of the eyes narrow, well rounded, and lower than the sector of the cheek in front of it, but lateral to this considerably broader and much higher than the cheek in front; palpebral lobes divided into two sectors—the inner slightly convex and rising gradually from the axis to a level slightly above that of the glabella, and an outer palpebral rim rising abruptly and steeply, and then curving over to become almost horizontal approaching the visual surface; outer edge of rim with a narrow slightly raised selvage; posterior edge of palpebral lobe opposite midpoint of lobes 1p, and anterior edge opposite the median tips of furrows 3p; visual surfaces of eyes almost vertical posteriorly, at ca. 15° to the vertical laterally, and ca. 20° to 25° anteriorly; in outline visual surfaces cover ca. 210 degrees of arc; approximately 190 quincuncially arranged lenses in the eye of the holotype; most posterior vertical row with 2 lenses and subsequent ones in sequence with 3, 3, 4, 4, 5, 5, 6, 6, 6, 6, 7, 7, 7, etc.; arrangement at anterior end is 3, 4, 5, 5, 6, 6, 7, 7, 7, 8, etc.; total number of rows 32, and the maximum number of lenses in a row 8; most lenses are ca. 0.25 mm in diameter, though some low on the eye as much as 0.30 mm; at the tops of rows in which the number of lenses is increased there is a small one ca. 0.15 mm; furrow present below the eye, narrowest at the back and becoming broader and slightly deeper toward the front.

Facial suture runs almost parallel to the anterior parts of the axial furrow and ca. 1.0 mm outside it; posterior to the eye it cuts along the base of the suborbital ridge and then swings outward and slightly forward in a gentle arc convex forward, and placing ω distinctly in front of ε .

Granulation over the whole upper surface of the cephalon except in all the furrows, which are smooth; granulation coarsest on the glabella, the inner parts of the palpebral lobes, and the cheeks behind the eyes, where there are ca. 20 granules per sq mm; slightly finer granules elsewhere inside the border furrows and along the posterior border and the crest of the genal spines; fine granules (40 to 50 per sq mm) around the borders.

Doublure widest in front where it is gently convex anteriorly but carries a broad, shallow, transverse arcuate furrow posteriorly (separating off a slightly upturned inner sector), presumably for the reception of the end of the pygidium; doublure immediately beneath anterior lobe of glabella with a sharp posterior edge (the hypostomal suture), but lateral to this with a sharp upfolded inner edge; outline of doublure has a distinct but variable break in curvature at the edge of hypostomal suture; doublure on genal spine convex; outer three-quarters or so of doublure (including genal spines) with shallow widely spaced pits, slightly elongated parallel with the outer margin; inner edge of flat portion with fine granules; upturned inner portion apparently smooth; facial suture sinuous across the doublure and reaches its inner margin in front of the genal spine; posterior doublure narrows rapidly from genal spine and disappears opposite the outer edge of the palpebral lobe; narrow articulatory furrow in the posterior edge of the cheek adaxial to fulcrum; doublure of occipital ring ca. one-quarter the length of the ring; apodemes all high and narrow (tr.) and arranged in two parallel rows; occipital apodeme with a concave posterior face, convex anterior face, and joined by a low elevation to the axis; apodeme 1p joined to the axis by a much wider ridge, and tending to be triangular in cross section; apodeme 2p spikelike, joined to the axis by a faint ridge, and almost linear in section; no apodemes 3p developed; hypostome unknown.

Thorax of eleven segments; axial rings flat, width/length ratio ca. 5:1; in dorsal view, rings bent slightly forward near the axial furrows; no lateral nodes on rings; articulating half ring half the length of the remainder of the segment, and separated off by a pronounced furrow pinching out laterally into the short (exsag.), wide (tr.) apodemes; pleurae straight and rectangular adaxial to the fulcra, then bent back strongly and narrowing to a point, but developing a broad flat anterior facet; anterior edge of pleura with a shallow linear articulatory furrow running from the axial furrow to beyond the fulcrum; at its outer end, an abrupt but slight increase in the height of the pleural facet; pleural spines on anterior segments short and straight, but longer and more sickle-shaped posteriorly; anterior pleural band well rounded in section (exsag.), with an almost vertical posterior slope, and midway between the axis and the fulcrum is one-third the length of the pleura; posterior band with a vertical posterior slope, and with a gentle anterior slope into the pleural furrow; granules coarsest (up to 0.125 mm diameter) on the rings and along the crests of both posterior and anterior bands; extremely delicate granules (0.03 mm in diameter) widely spaced in the pleural furrows, and possibly along the posterior face of the articulating half rings; slightly coarser granules closely packed on the pleural facets; ventral surface of thorax unknown.

Pygidia flattened in both anterior and lateral profiles; faintly upturned posteriorly; divisible into two types according to presence or absence of a caudal spine; both types with eight (less commonly seven) pleurae, and twelve to thirteen (rarely eleven or fourteen) axial rings, although the most posterior two usually almost indistinguishable; anterior ring with a pronounced posterior median excavation, and second, third, and occasionally fourth rings with markedly diminished excavations; six or seven interpleural furrows exactly joining the most anterior six or seven axial furrows; pleural furrows with almost vertical anterior slopes and gentle posterior slopes, becoming rapidly shallower crossing the inner edge of the doublure, and fading away 0.5 to 1.0 mm from the margin; interpleural ridges very narrow and shallow; posterior band much lower than the succeeding anterior band, and at the fulcrum is ca. one-third the length (exsag.) of its own anterior band; ornament of the rings and pleural bands and furrows similar to that of the thorax; border and spine with closely spaced granules of same size as bands; articulating facet low, and its lower edge with an abrupt change in outline at the junction with the doublure.

Pygidia that lack caudal spines show wide variation in outline, as shown on plate 16, figures 1-13; larger specimens longer relative to their widths than smaller ones; specimens that bear spines are proportionately narrower at all growth stages represented; caudal spine with a flat base and a triangular cross section.

Doublure sharply inflected around the margin, with a broad flattened outer band, and a much narrower inner band gently upturned at ca. 30° to 40°; posteriorly doublure reaches to the end of the axis; appressed appendifers present on seven segments; anterior appendifers massive and directed downward and inward, but subsequent ones diminishing rapidly in size; all appendifers reach half way from the axial furrow to the median line.

Remarks.—The collections contain only one

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type of dalmanitid cephalon, but the two distinct types of pygidia occur in approximately equal numbers. Although the pygidia are easily assigned to one group or the other, the two groups have many features in common. Sexual dimorphism seems to be the only satisfactory explanation of the data, and hence I have described all the material as a single species.

From all described American species that are known from both the cephalon and pygidium, D. rutellum can be distinguished by several features. The most important of these are the ornament of the cephalon (and thorax); the position of the anterior part of the facial suture with respect to the axial furrow; the shape and position of the palpebral lobe; the size of the visual surface of the eye and the arrangement of the lenses; the length of the genal spines; the shape of the rings of the thorax; the number of rings and pleurae on the pygidium; the strength of the interpleural furrows on the pygidium; and the caudal spine.

Richardson (1949) described a new species, D. oklahomae, from the "probably Silurian, probably Henryhouse Shale." The source of the single specimen on which it was based has been discussed by Amsden (1956), who concluded that it is probably a Haragan form. It is readily distinguished from D. rutellum by its narrower borders and more protuberant and differently ornamented glabella.

The species most likely to be confused with it are D. brevigladiolus Foerste, from the Hoplophragma zone, Lilley Member, Western Union Formation of Ohio; and D. limulurus (Green), from the Rochester Shale of New York (not the Lockport Formation, as stated by Delo, 1940, p. 44). D. brevigladiolus is distinguished by its slightly finer ornament on the glabella, a narrower (tr.) anterior glabellar lobe relative to its length, shorter (exsag.) palpebral lobes, a longer and flatter caudal spine, and much stronger interpleural furrows on the pygidium. D. limulurus has distinctly finer granulation on all parts of the test; a shorter anterior border; a wider cheek between the eyes and the border furrow; smaller eyes (0.25 to 0.3 of the length of the glabella as compared with ca. 0.45 in D. rutellum), flatter anterior bands on the thoracic pleurae; shallower pleural and deeper interpleural furrows on the pygidium; and longer caudal spine.

The incompletely known D. stewartae, from the Devonian Little Saline Limestone of Missouri, is represented by two broken pygidial internal molds. The shape and number of segments are similar to *D. rutellum*, but no conclusions can be drawn from such inadequate data.

Among overseas species, the closest is *D. myops* (König) from the Wenlock Limestone, Dudley, but it has a shorter anterior border; facial suture in the preglabellar furrow; smaller eyes and palpebral lobes; larger tubercles on the glabella; nodes at the ends of thoracic rings; shallower pleural and deeper interpleural furrows on the pygidium; a broader unfurrowed pygidial border; and a more prominent caudal spine.

Family ODONTOPLEURIDAE Burmeister, 1843

Subfamily ODONTOPLEURINAE Burmeister, 1843

Genus Leonaspis Richter and Richter, 1917

Type species.—Odontopleura leonhardi Barrande, 1846, from the Kopanina Limestone (Ludlovian) of Czechoslovakia.

Remarks.—Leonas pis has been discussed adequately by Whittington (1956a, 1956b).

Leonaspis sp. Pl. 19, fig. 9

Remarks.—A single poorly preserved cheek is referred to Leonaspis. It is known only from the lower surface, and no useful comparisons can be made.

Material.—Specimen OU 5609, from upper 2 feet of Henryhouse Formation, west of U. S. Highway 77, NW 1/4 sec. 30, T. 1 S., R. 2 E., Murray County.

Genus Dudleyaspis Prantl and Přibyl, 1949

Type species.—Acidaspis quinquespinosa Lake, from the Wenlock Limestone of Dudley, England.

Remarks.—Dudleyaspis is here interpreted in the sense of Whittington (1956b, p. 234-235), except for the following points: (1) The number of spines on the posterior border and occipital ring is variable, although the presence of spines, and especially the median occipital spine, is considered to be diagnostic. (2) The occipital ring and the axial lobe of the thorax are particularly wide. (3) The lateral lobes of the occipital ring are present in both known species, but they are not completely isolated (pl. 19, figs. 3, 4). (4)

The posterior pleural spines on all thoracic segments are transverse and gently tapering. Those on the anterior segments are not modified. (5) The ornament on the thoracic segments consists of multiple granules comparable in size to those of the cephalon.

Range.—As here interpreted, the genus is at present known only from England and North America, where it occurs in the upper Wenlockian and lower Ludlovian.

Dudleyaspis desolator, new species

Pl. 18, figs. 5-7; pl. 19, figs. 3-8

Types.—All types are from sec. 4, T. 2 N., R. 6 E., Pontotoc County, as follows: holotype OU 5601, from SE 1/4 SE 1/4; paratype OU 3628, from NE 1/4 SW 1/4 SE 1/4; paratype OU 5602, from NW 1/4 SE 1/4; paratype OU 5603, from SE 1/4 SW 1/4.

Description .- All specimens somewhat compressed, but originally must have been moderately arched in both lateral and longitudinal profiles; occipital ring (exclusive of spine) 0.2 the length of the cephalon, measured with crest of glabella approximately horizontal; anterior and posterior occipital bands present, each about half the length (sag.) of the ring; boundary between the two bands lightly impressed; occipital lobes present, but poorly defined by a shallow furrow and a break in granulation along their inner, but not their posterior, edges; posterior edge of the occipital ring produced back into a large broadly based median spine 1 to 1.5 times the length of the ring itself, and a pair of much smaller spines, one on either side, given off from behind the outer edge of the anterior band; small rounded median tubercle on the boundary between the two bands, or just in front of it and carrying a tetrad of depressions in its tip (Whittington, 1956a, pl. 2. fig. 23); occipital furrow is moderately deep behind lobes 1p, but shallowing abruptly medially; normal cephalic granules present in occipital furrow between the inner ends of glabellar furrows 1p; axial furrows bounding the occipital ring and glabellar lobes 1p and 2p weak, marked mainly by the absence of ornament; forward of this these outlines indistinct, and granulation not interrupted; outline of glabella defined by changes in slope of the surface rather than by a definite furrow; glabella widest at the occipital ring and tapers gradually to slightly beyond the midpoint of lobe 2p, where rate of taper increases; glabellar furrow 1p variably impressed and shaped—in

largest specimen represented by a faint broad depression with only minor interruption of the surface granulation, but in other specimens a slight but sharp groove without granulation at the anterior end of the furrow, becoming broader, less definite, and granulated posteriorly; in general, outer part of furrow 1p almost perpendicular to axial furrow, and separated by a strong flexure from its inner part, which is almost parallel to the longitudinal axis; furrows 2p at least as strongly impressed as 1p, and in all four specimens without granulation in their sharply impressed outer courses, which are perpendicular to the axial furrow; inner part of 2p broader, granulated, and more vaguely defined; furrow 3p present in all cases, but short and very lightly impressed; pair of dimples present near the axis of largest specimen at midlength of lobe 1p. Eye ridge straight, strong, and fading away against the anterior edge of the glabella; ornament similar to that of surrounding areas, but ridge defined by a linear break in the ornament on both sides, the gap being most marked at the adorbital end on the inner side and at the aborbital end on the outer side.

Rostral suture equal in width to the glabellar width at furrows 3p; connective sutures slightly divergent; anterior sutural ridge faint, running forward and slightly inward from the eye to meet the border furrow above the third or fourth marginal spine lateral to the rostral plate; posterior sutural ridge a little stronger, developing from the inner side of the palpebral lobe and following a markedly sigmoid course to the base of the genal spine; facial suture itself not observed. Eye globular, approximately two-thirds of a sphere, not stalked, situated half way (tr.) between the axial furrow and the middle of the border furrow, and with its anterior edge immediately behind a line joining the anterior edges of furrows 1p.

Anterior and lateral borders forming a well-rounded ridge, fading away in front of the glabella, and becoming distinctly weaker near the genal spine; anterolateral spine fringe formed of ten spines on either side; most lateral spines curved downward and outward, and "webbed" together slightly by a downgrowth of the border; medial spines straight and short; spines taper abruptly to points at their tips; three small pustulelike spines on the upper surface of the border, the largest being the posterior one above fringe spine 3 or between 3 and 4, the second above 5 or between 5 and 6, and the smallest between 7 and 8; librigenal spine similar in size and shape to those of the type species; posterior border well

rounded, but not so strong as lateral border, and with a single short spine just lateral to the position of the eye.

Ornament remarkably consistent; granules of two basic sizes present on dorsal surface; primary granules well rounded, smallest on the glabella, slightly larger on the cheeks inside the eye ridges, and larger still outside the eye ridges; secondary granules much finer and scattered irregularly between the primaries; anterior and lateral border furrows granulated similarly to surrounding areas, but granulation of posterior border furrow indeterminate due to poor preservation; outer face of border with finer granules than the upper face; approximately six pairs of slightly enlarged spines in rows down median glabellar lobe (pl. 19, fig. 5); librigenal and median occipital spines with scattered, rather large, posteriorly directed microspines, separated by granules; spines of the border fringe with a single regular to irregular row of granules down their outer edges, and the remainder of the outer face covered with a mist of mircrogranules.

Thorax and pygidium unknown.

Remarks.—Dudleyaspis desolator shows little variation in the limited amount of material available. The differences in the spread of the border spines is great but can be explained in terms of the ages of the individuals concerned.

D. desolator can be distinguished from the type species as follows:

D. desolator

- 1. Two spine pairs plus median spine on posterior margin of cephalon.
- 2. Densely spaced granules of two main orders.
- 3. Robust genal spines.
- 4. Weak sutural ridges.
- - 3. Weak genal spines.
- D. quinquespinosa 1. Four spine pairs plus median spine on posterior margin of cephalon.
- 2. More widely spaced granules of a variety of sizes.
 - 4. Strong sutural ridges.
- D. quinquespinosa has been recorded from America by van Ingen (1901b, p. 50, fig. 12) in the St. Clair Limestone of Arkansas. I have not examined the specimen, and it is not possible to make certain identification from the published figure. The only other described American species which might belong in Dudleyaspis is Acidaspis vanhornei Weller, from the Niagaran dolomites of Bridgeport, Illinois (Weller, 1907, p. 251, pl. 23, figs. 3-4).

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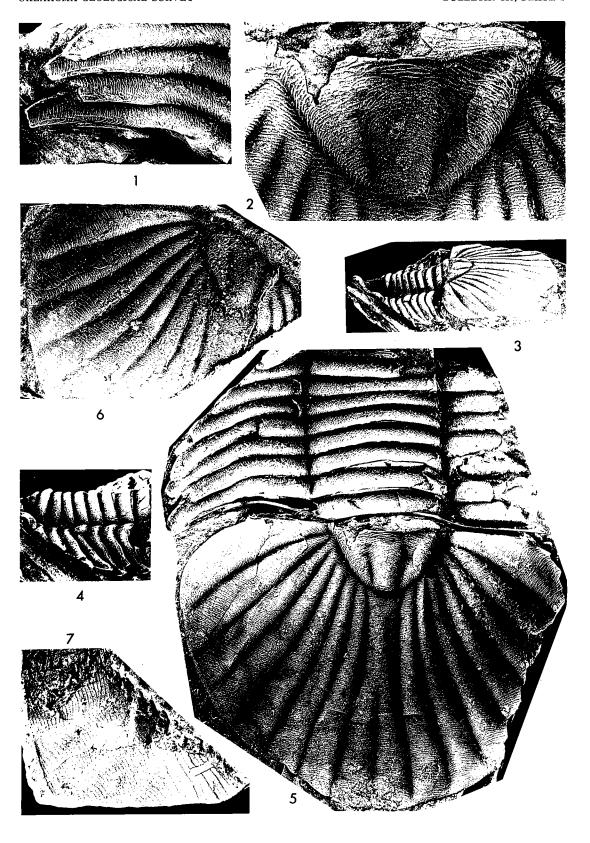
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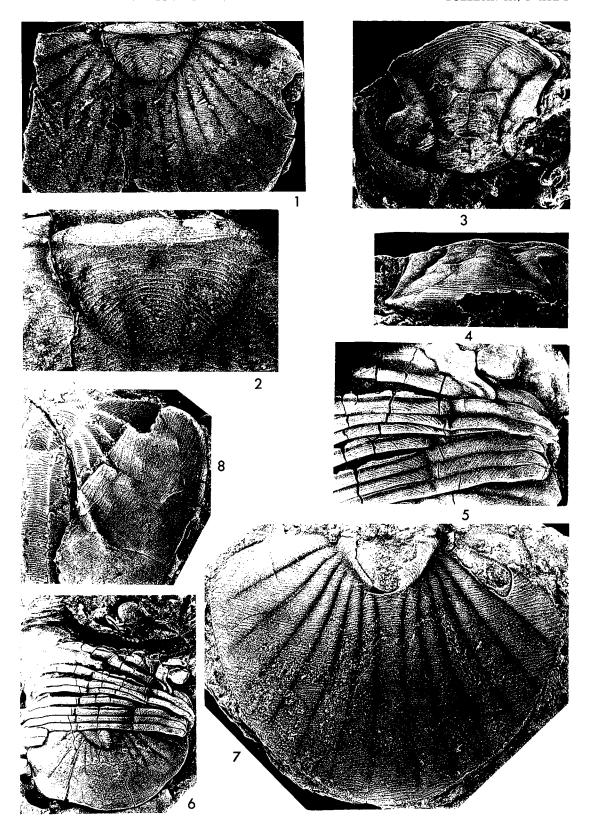
HENRYHOUSE TRILOBITES

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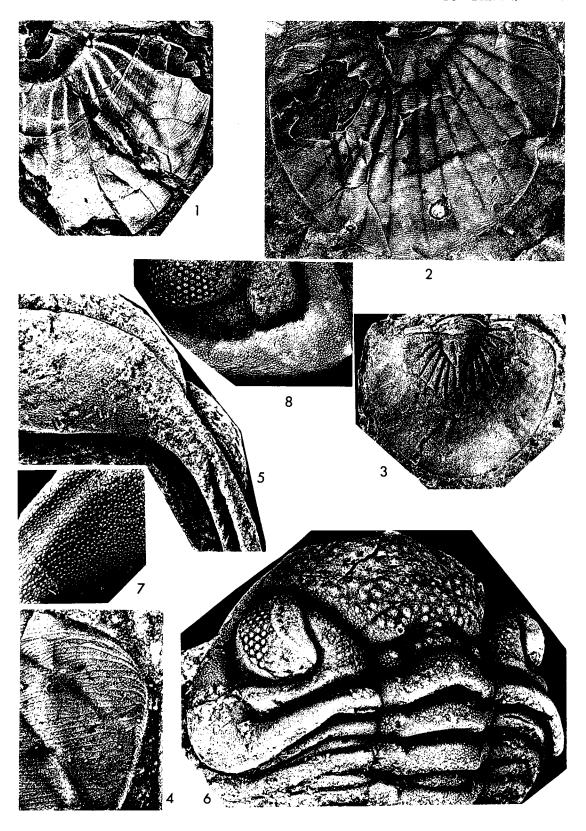


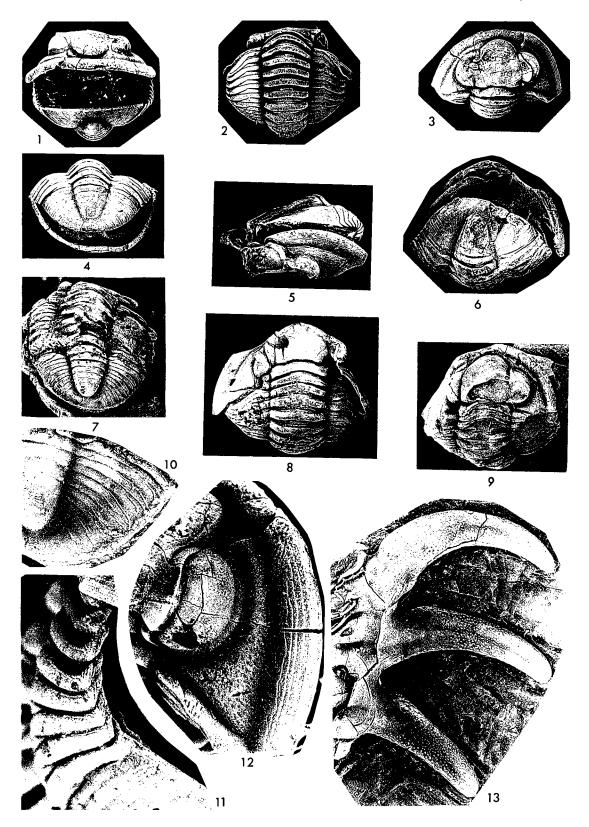
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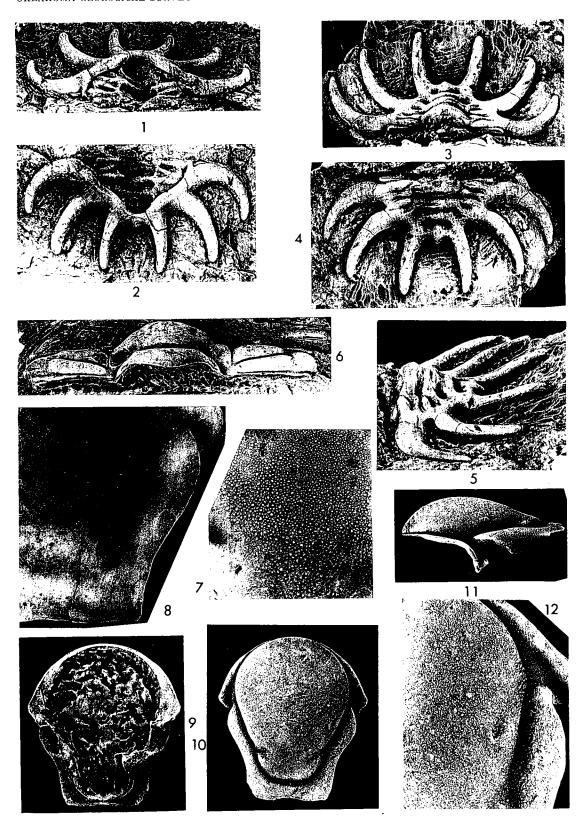


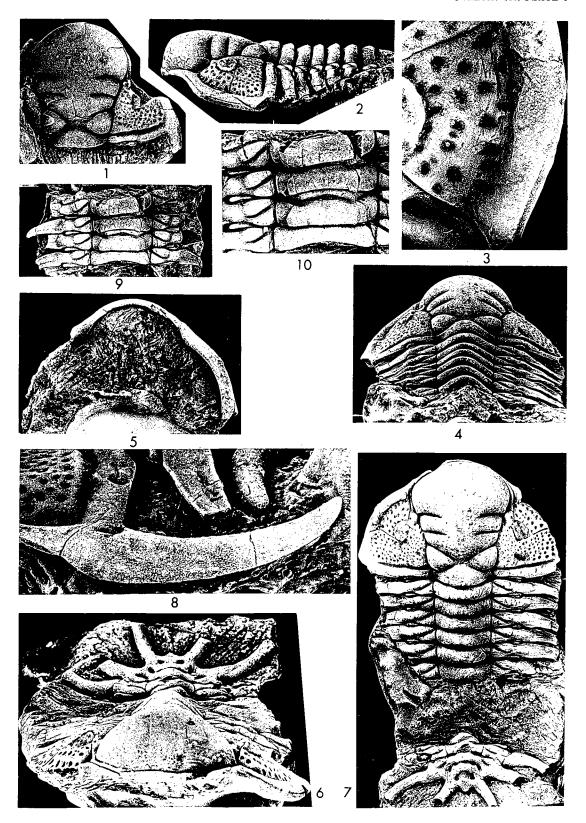
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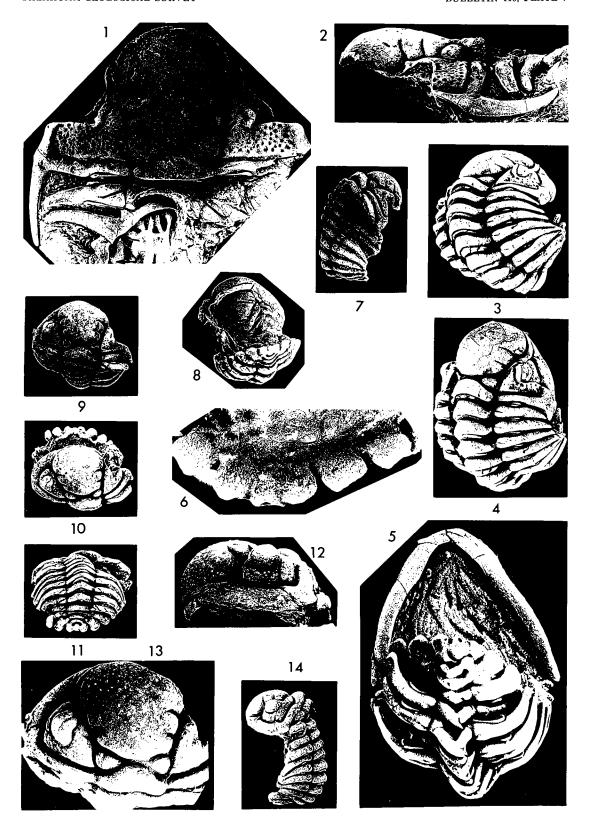


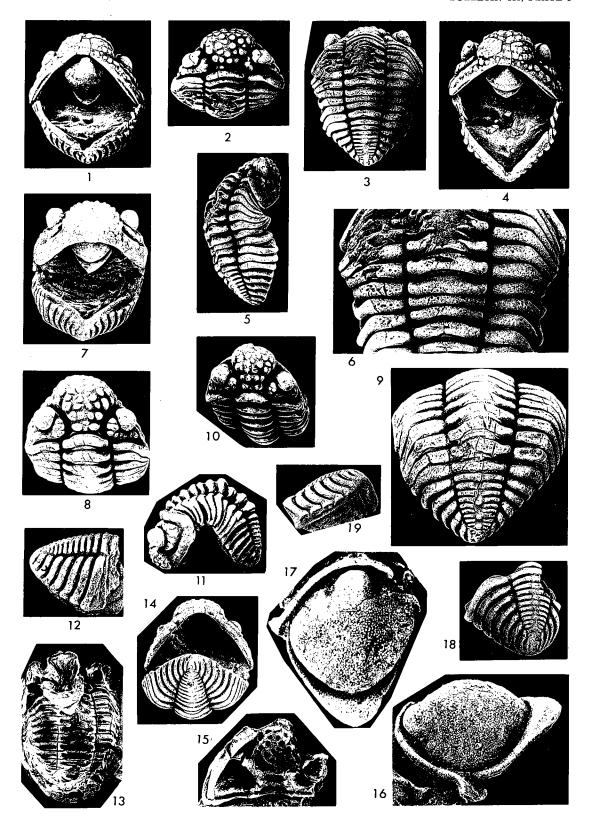
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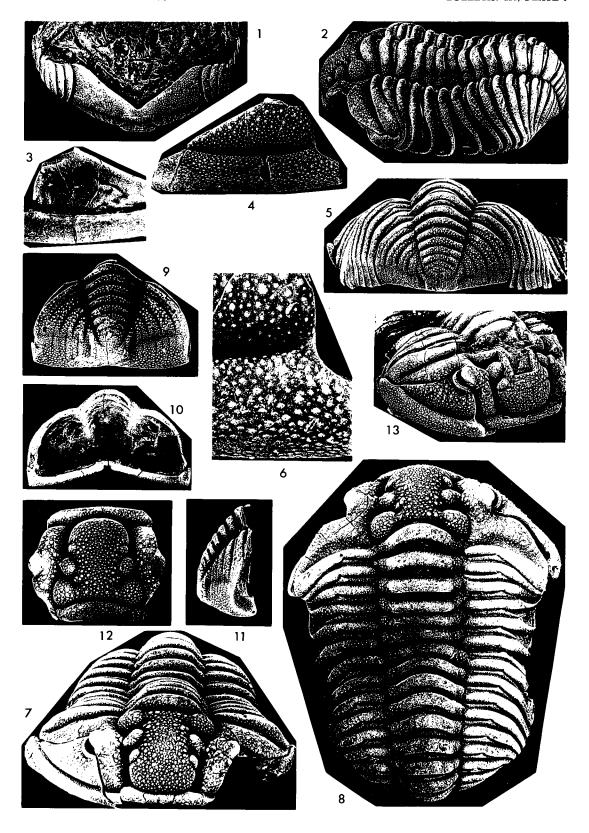


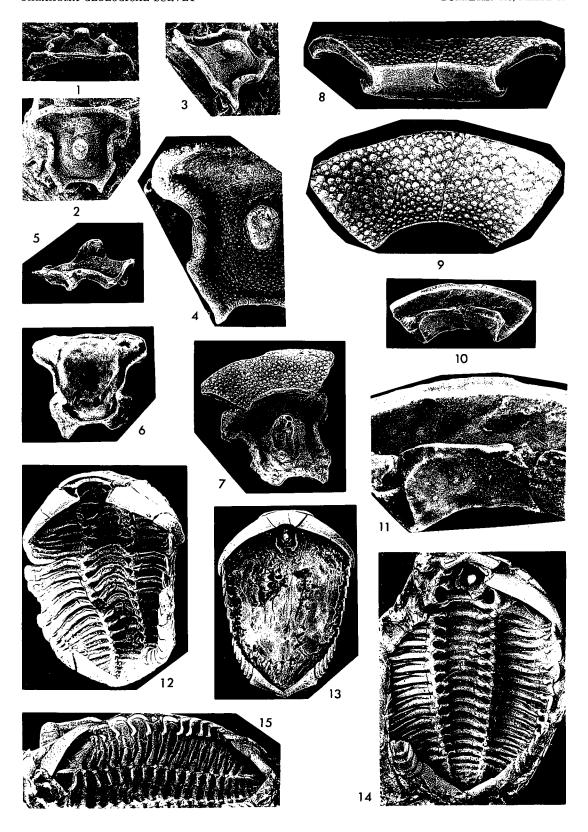
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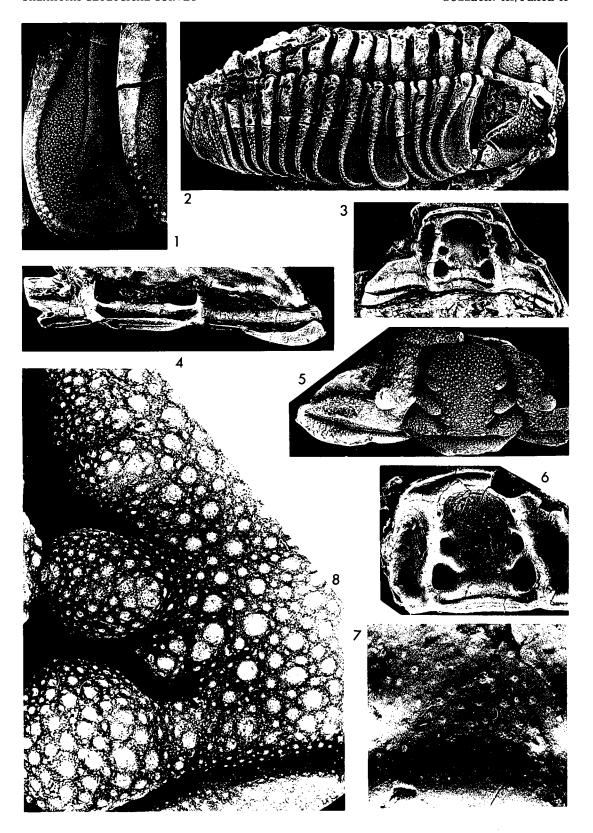


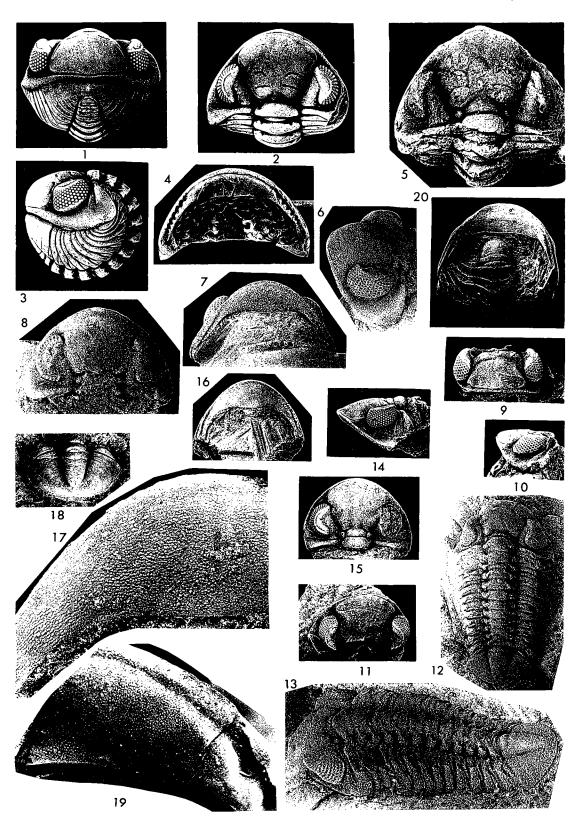
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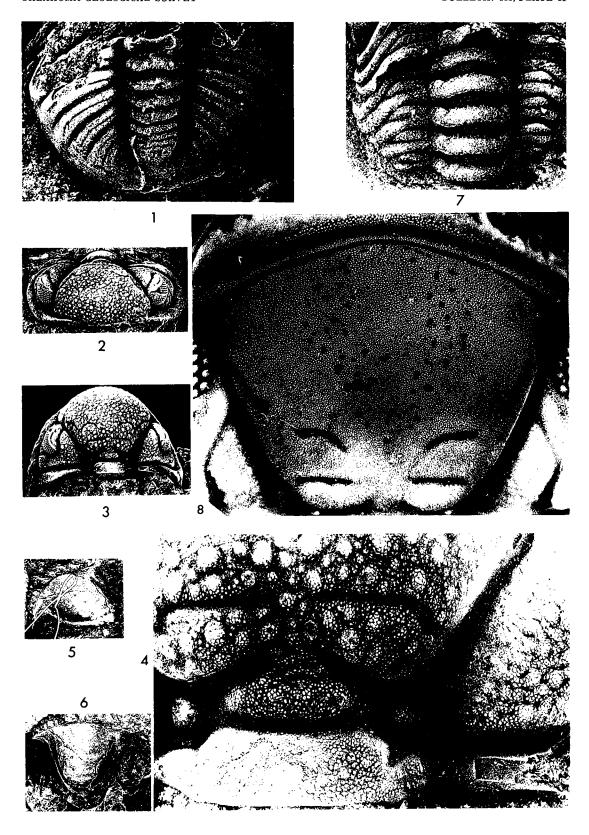


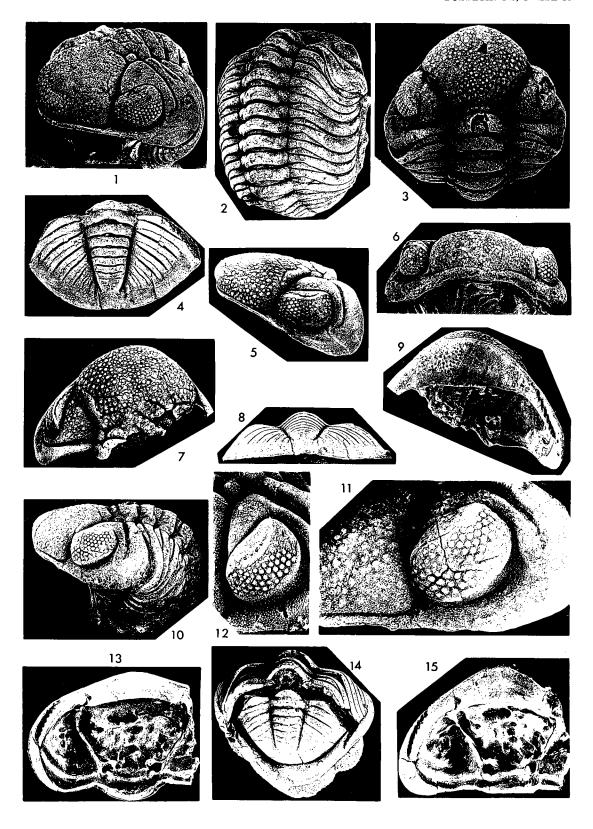
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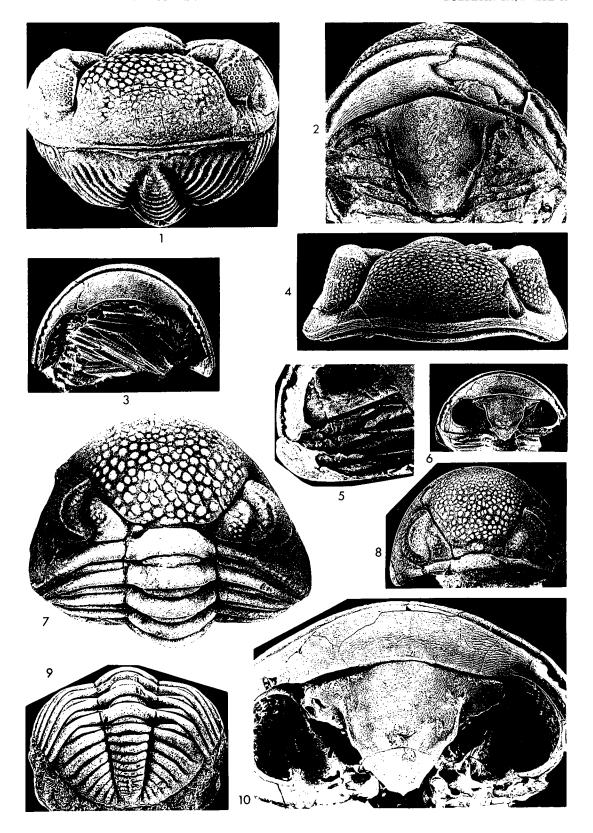


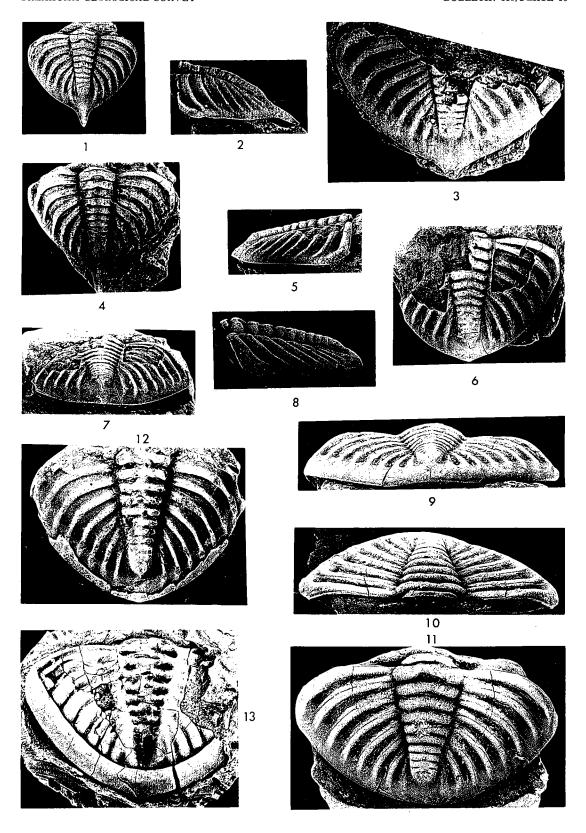
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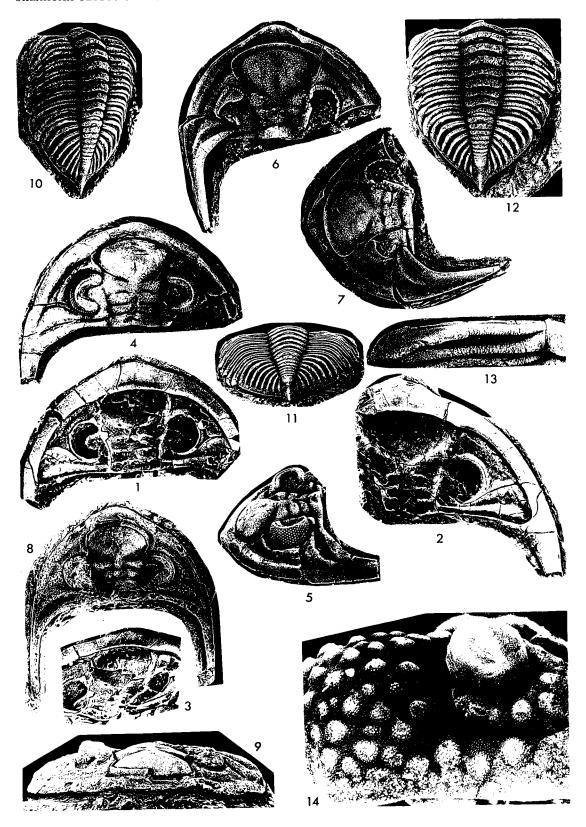
Dalmanites rutellum, new species

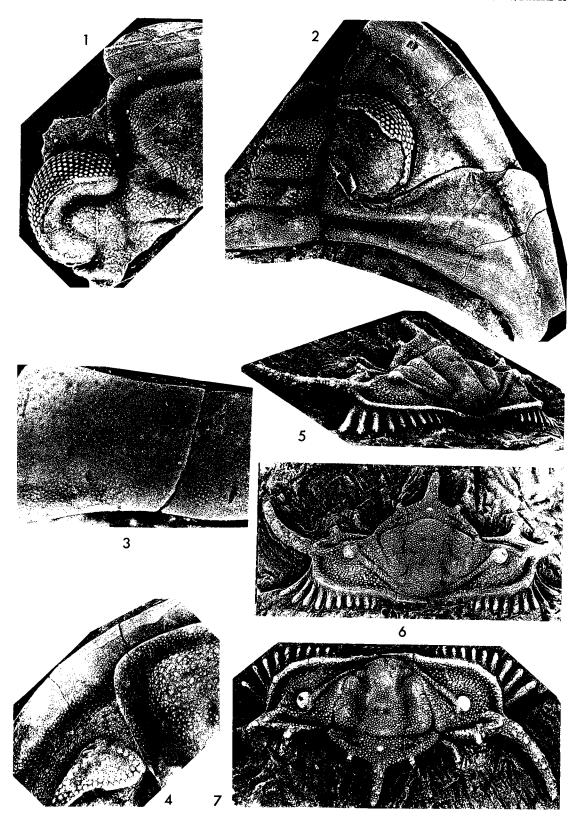
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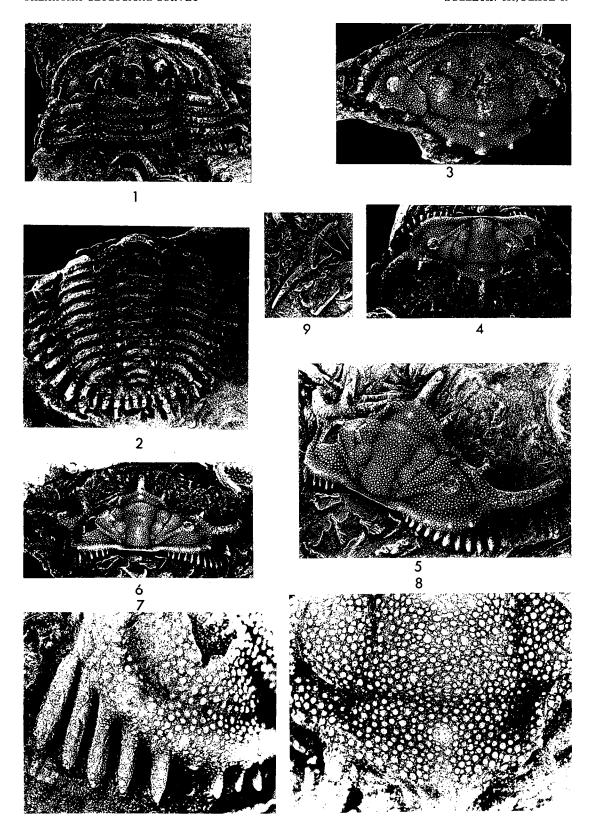


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