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TRILOBITES OF THE HARAGAN, BOIS D'ARC AND FRISCO FORMATIONS (EARLY DEVONIAN) ARBUCKLE MOUNTAINS REGION, OKLAHOMA

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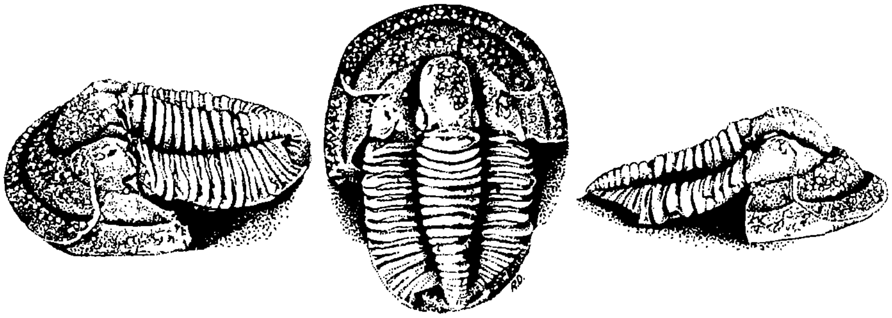

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Title Page Illustration

Ink drawing by Roy D. Davis showing oblique, dorsal, and lateral views of *Cordania falcata* Whittington, from the Haragan Formation. This specimen, also illustrated on plate 5, was collected from the Old Hunton Townsite.

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TRILOBITES OF THE HARAGAN, BOIS D'ARC AND FRISCO FORMATIONS (EARLY DEVONIAN) ARBUCKLE MOUNTAINS REGION, OKLAHOMA

K. S. W. CAMPBELL[1]

Abstract—The trilobite fauna of the Early Devonian in Oklahoma includes 15 species from the Haragan Formation, 18 from the Bois d'Arc Formation, and 8 from the Frisco Formation. Five species are found in both the Haragan and Bois d'Arc Formations, but the Frisco Formation fauna is entirely distinct. Most of the common species have been recognized and described previously, but 7 less common forms are designated as new species, and 2 new subspecies are named. Also named and diagnosed are new dalmanitinid genera and subgenera *Huntonia (Huntonia)*, with type species *Dalmanites lingulifer* Ulrich and Delo; *Huntonia (Prosocephalus)*, with type species *H. (Prosocephalus) xylabion*, new species; and *Phalangocephalus*, with type species *Dalmanites dentata* Barrett.

The taxonomy of the Phacopinae is discussed in detail, and a critical assessment of recent theory and practice in this field is presented. The relationship between the Synphoriidae and Dalmanitidae is examined, and new criteria are proposed for their recognition. Functional analysis of the Dalmanitidae is used to provide a basis for the taxonomy of that group.

One of the most remarkable features of this trilobite fauna is the abundance of dimorphic (and trimorphic) species it contains. No fewer than five species are clearly dimorphic, and some previously described "species" of *Huntonia (Huntonia)* probably represent dimorphic pairs.

Stratigraphically, there is some evidence in the trilobite fauna to support the view that the Haragan is slightly older than the New Scotland–Kalkberg of New York and the Birdsong-Ross of Tennessee. The Fittstown Member and the upper section of the Cravatt Member of the Bois d'Arc may be equivalent in part to the Birdsong-Ross. The Frisco trilobites indicate a Deerparkian age for that formation.

Biogeographically, these faunas may be regarded as a filtered Appalachian assemblage, together with some elements from the Great Basin and perhaps beyond. These results are compared with those obtained from studies of ostracods and brachiopods.

INTRODUCTION

On first inspection, the trilobite faunas of the Haragan and Bois d'Arc Formations appear to lack diversity and to be dominated by one or two species. Although the latter is certainly true, diversity is moderately high. Many genera, however, are represented by fewer than five specimens.

These Oklahoma faunas have not previously been studied systematically, although isolated species have been described by Delo (1935, 1940), Richardson (1949), and Whittington (1956b, 1960). For this reason, to put the Haragan, Bois d'Arc, and Frisco trilobites in the context of North American Early Devonian trilobites in general, it has been necessary to study several described species from other states, particularly the phacopids and the dalmanitinids. Dr. Niles Eldredge (1973), whose work to some extent overlaps this study, published a monograph on the phacopids. Work on the dalmanitinids, however, except for the synphoriinids, which have been revised by Dr. Pierre Lespérance

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(1975), is still in a primitive state, and there is an urgent need for a revision of all the Early Devonian species recorded by Delo (1940). I have examined the types of as many dalmanitinids as possible, and where necessary for present purposes I have described and figured them.

Collections used in the present study are those of the Oklahoma Geological Survey and The University of Oklahoma, supplemented by smaller but significant collections from the Smithsonian Institution and Yale University. These collections have been accumulated over the years by stratigraphers and by paleontologists who were mainly interested in the brachiopods, and because of this it is possible that the smaller and less complete species are underrepresented. This may also partially explain the small numbers of proetids, which dissociate easily. By contrast, the small though spectacular otarionids, which are often preserved whole, are quite common in the collections.

Preservation of specimens in the Haragan Formation is in soft, marly matrix similar to that of the Henryhouse (see Campbell, 1967), and the matrix can be removed from the exoskeletons with vibrotool and airabrasive treatment. Specimens from the Cravatt Member and the Frisco Formation are usually in a much harder limy marl and do not yield to airabrasive treatment. As their exoskeletons often flake off with the external mold, details of the fine structure are sometimes missing from descriptions of these species. The Fittstown Member specimens are fragmentary but are relatively easily separated from the coarse matrix by mechanical means, and surface detail is good.

In preparing this bulletin, a number of fellow workers assisted me by offering specimens, information, references, and discussion of various problems. Dr. T. W. Amsden, of the Oklahoma Geological Survey, and Prof. P. K. Sutherland, of The University of Oklahoma, provided most of the collections. Their collections were supplemented by specimens from the U.S. National Museum, where Dr. Porter Kier, Dr. Richard Grant, and Dr. Frederick Collier were most generous in their cooperation. Prof. Lawrence Walker, of the University of Memphis, collected specimens of *Phacops birdsongensis* from Big Sandy River and made them available, together with other specimens.

Dr. Niles Eldredge, of the American Museum of Natural History, discussed numerous problems of phacopid and dalmanitinid taxonomy with me, provided preprints of some of his papers, and sent casts and original specimens of *Phalangocephalus dentatus* for description as well as other casts for comparative work. Prof. Pierre Lespérance, of Montreal University, discussed problems of dalmanitinid and synphoriinid taxonomy and sent preprints of his papers. Dr. Allen Ormiston, of Amoco Production Co., contributed information on several points of taxonomy and biogeography, and Dr. Euan Clarkson, of Edinburgh University, helped clarify my views on the structure of the lenses of phacopids. In matters of interpretation I have not always been able to reach agreement with all these colleagues, but a remarkable degree of cooperation has certainly allowed our differences to be aired in a beneficial way.

Prof. Bernhard Kummel, of Harvard University; Prof. Harry Whittington and Dr. Barry Rickards, both of Cambridge University; Dr. Gunnar Henningsmoen, of the Palaeontological Museum, Oslo; Dr. Radvan Horný, of the Narodni Museum, Prague; Dr. Ivo Chlupáč, of the Geological Survey, Prague; Dr. Z. A. Maksimova, of VNIGRI, Leningrad; Dr. Donald Fisher and Dr. Robert Conrad, of the New York State Museum; Dr. Matthew Nitecki, of the Field Museum, Chicago; Dr. Alex Ritchie, of the Sydney Museum; and Mr. Lawrence Sherwin, of the New South Wales Geological Survey, have been generous in making specimens in their keeping available for study.

In Canberra, Mrs. Robyn Lawrie did much of the preliminary work on the phacopid eyes and devised the method of representing the statistical pattern of the lenses. She and Mr. D. J. Holloway undertook a preliminary sorting of the multitude of separated dalmanitinid cephala and pygidia. Dr. Peter Jell engaged in many discussions and read and made many changes to the manuscript. The photographs of the plates are largely the work of Mr. Leo Seeuwen, and the text-figures were drawn by Mr. Gregory Harper and Dr. Jell. The typing of the manuscript over long periods of time and in several drafts was undertaken by Linda Warren, Anne Kilner, and Pamela Carle.

To all these colleagues and fellow workers I have an obvious debt, which I take pleasure in acknowledging.

HARAGAN–BOIS D'ARC TRILOBITES

Haragan Species

Scutelluid, genus and species undet.	scarce
Paciphacops (Paciphacops) raymondi (Delo)	very common
Reedops deckeri Delo	common
Huntonia (Huntonia) lingulifer (Ulrich and Delo)	common
Huntonia (Huntonia) huntonensis (Ulrich and Delo)	common
Huntonia (Huntonia) oklahomae (Richardson)	common
Huntonia (Huntonia), new form	uncommon
Huntonia (Huntonia) purduei purduei (Dunbar)	uncommon
"Odontochile" taffi (Ulrich and Delo)	scarce
Otarion axitiosum Campbell, new species	common
Cordania falcata Whittington	common
Dechenellid, genus and species undet.	scarce
Leonaspis williamsi Whittington	common
Ceratonurus sp.	scarce
Dicranurus hamatus elegantus Campbell, new subspecies	uncommon
Echinolichas coccymelum Campbell, new species	uncommon

The trilobites in this formation are well preserved, with a large proportion of them retaining articulation in most or all of the exoskeleton. In general, the larger the specimen, the less the probability of its being recovered in an articulated state.

The fauna is dominated by the Phacopidae. In fact, *P. (Paciphacops) raymondi* is more numerous than all the other species together. *Reedops deckeri* is also present in significant numbers. Estimates indicate the second most abundant family, the Dalmanitinidae, to be represented by less than one-quarter the number of specimens of phacopids, although their precise number is difficult to determine because most of them are dissociated. Although they are more diverse than the Phacopidae, the number of species of dalmanitinids listed will have to be reduced if the suggestion that some of the named forms are sexual dimorphs proves valid.

The remainder of the fauna is rather sparse, with four of the species represented by only one or two specimens. The possibility exists, however, that further detailed collecting may produce other rare species of biogeographical significance.

Most of the specimens were recovered from the Old Hunton Townsite or the White Mound localities, where they seem to be distributed through the section. Small numbers of specimens are recorded from 12 other localities, some of them having more than 1 horizon. Because these collections are so small, it is difficult to interpret absences of species. Putting all the information together, there is no indication that the fauna within the formation can be zoned on the basis of the trilobites. Certainly, the more abundant species range through a large part of the formation.

Bois d'Arc (Cravatt Member) Species

Paciphacops (Paciphacops) raymondi (Delo)	uncommon
Paciphacops (Paciphacops) cf.birdsongensis (Delo)	scarce
Huntonia (Huntonia) purduei purduei (Ulrich and Delo)	uncommon
Huntonia (Huntonia) lingulifer (Ulrich and Delo)	uncommon
Odontochile syncrama Campbell, new species	scarce
Dechenellid, genus and species undet.	scarce
Cheirurid, genus and species undet.	scarce

The fauna of the Cravatt Member of the Bois d'Arc Formation is sparse in comparison with that of the Haragan Formation and is known from many fewer localities. *Paciphacops* is the most common genus and occurs at the largest number of localities, about 25. *Huntonia (Huntonia)* is the second most abundant genus, and almost the entire collection of this genus was recovered from one locality. The remainder of the species are represented by single specimens.

Bois d'Arc (Fittstown Member) Species

Paciphacops (Paciphacops) invius Campbell, new species	uncommon
Paciphacops (Paciphacops) cf. *birdsongensis* (Delo)	scarce
Huntonia (Huntonia) purduei fittstownensis Campbell, new subspecies	uncommon
Huntonia (Prosocephalus) xylabion Campbell, new species	uncommon
Odontochile syncrama Campbell, new species	scarce
Phalangocephalus rutabulum Campbell, new species	scarce
Calymenid, genus and species undet.	scarce
Coniproetus sp.	scarce
Otarion cf. *axitiosum* Campbell, new species	common
Dicranurus hamatus elegantus Campbell, new subspecies	scarce

The Fittstown Member of the Bois d'Arc Formation is composed mainly of coarse calcareous clastics. The fauna is not widespread in the Fittstown: most of the specimens are from only a few localities, and one locality, Amsden's P16, provided the entire material of five of the above species. Although this member has two-thirds as many species as the Haragan, the total collection from it is only a small fraction of the Haragan specimens. Presumably the number of niches available for trilobite colonization was greater in the area where coarse-grained sediment was accumulating. This implies patches where quiet conditions existed, perhaps for only short periods. The finer sediment formed in such areas has been removed by turbulence, but the fossils from it were preserved by redeposition in the concomitant coarse sediment.

All the specimens are dissociated, but there is no size sorting. At locality P16, *H. (H.) purduei fittstownensis* pygidia are aoong the largest trilobite elements known from the Devonian, and although they are broken the fragments are large and have well-preserved surfaces. On the same slabs of rock there are numerous cranidia and cheeks of *Otarion* cf. *axitiosum* showing fine detail. These are among the smallest trilobites in the collections. The specimens do not lie in bedding planes but are oriented at all angles, suggesting that deposition occurred during a time of turbulent action, although the unabraded surfaces and the relatively complete nature of the specimens indicate that the turbulence was of short duration. Obviously otarionids could not have survived in areas where the water was to any degree turbulent, and presumably bottom conditions, at least in pools on the calcarenite surface, were normally quiet; but periodically the whole area must have been worked over and the sediment picked up and dumped without much further reworking.

Frisco Trilobites

Paciphacops (Paciphacops) Campbell, new species	uncommon
Paciphacops (Viaphacops) cristata cf. *bombifrons* (Hall)	scarce
Paciphacops (Viaphacops) Campbell, new species	scarce
Odontochile ceraunus Campbell, new species	uncommon
Dalmanitacea, genus and species undet.	scarce
?*Proetus*, species undet.	scarce
Otarion sp.	common
?*Terataspis* sp.	scarce

The Frisco fauna is meager, with most of the specimens having been recovered from a single locality, Amsden's S6. The specimens from this locality are all fragmentary, and it has been impossible to reconstruct two of the larger species with any degree of satisfaction. As with the Fittstown fauna, large and small species are commingled in the same rock, and the environments of deposition were probably comparable.

CORRELATIONS AND AGES

Haragan–Bois d'Arc Formations

Because previous work has established the facies relations between the Haragan and Bois d'Arc, trilobites from these two formations are considered as a single unit. It should be noted here, however, that the Fittstown Member and the upper part of the Cravatt Member of the Bois d'Arc are younger than most of the Haragan, though the age difference is very slight. Trilobites contribute little new information to the dating of these units, and all that is possible is a general comparison between these faunas and those in the northeastern states. There is a general similarity between the Haragan–Bois d'Arc faunas and the faunas of the New Scotland –Kalkberg rocks of New York and their equivalents in the northeastern states. These are set out below:

Haragan–Bois d'Arc	New Scotland–Kalkberg
P. (Paciphacops) raymondi (Delo)	*P. (Paciphacops) logani* (Hall)
Odontochile syncrama Campbell, new species	*Odontochile litchfieldensis* mondi (Delo)
Cordania falcata Whittington	*Cordania cyclurus* (Hall and Clarke)
Leonaspis williamsi Whittington	*Leonaspis tuberculatus* (Hall)
Dicranurus hamatus elegantus Campbell, new subspecies	*Dicranurus hamatus* (Hall)
Echinolichas coccymelum Campbell, new species	*Echinolichas bigsbyi* (Hall)

Although these comparisons do not indicate contemporaneity, and in fact may indicate the opposite (see discussion on Biogeography and Paleoecology, following) the trilobites offer a small amount of evidence indicating that any age discrepancy is probably slight. *P. (Paciphacops) raymondi* is different from *P. (P.) logani* in some characters that can be organized into chronoclines, but the differences are minor. For example, the smaller angle of divergence of the axial furrows and the low sclera between the lenses on the large-eyed morph in *raymondi* suggest that species is less advanced than *logani*. *P. (P.) invius* from the Fittstown Member is more advanced in ornament pattern and divergence of the axial furrow than *P. (P.) logani,* but it is less advanced in eye morphology and in the structure of the intercalatory ring than *P. logani* subsp. A of Eldredge (1973, p. 301) from the Becraft Formation. A few specimens close to *P. (P.) birdsongensis* occur in the Fittstown Member, and *birdsongensis* is more advanced than *logani* in eye morphology. The Cravatt Member contains specimens similar to *raymondi,* as well as several individuals that clearly belong to *P. (Paciphacops)* but that are much closer to *birdsongensis* than to *raymondi*. Their eye morphology is more advanced than that of *birdsongensis,* with the 17 file form having only 60-65 lenses. *Phalangocephalus rutabulum* from the Fittstown Member is a less advanced species than *P. dentatus* from the Point Jervis Limestone in that it has many fewer marginal cephalic spines. If "advanced" in the above arguments may be equated with b"younger," the Haragan and Bois d'Arc Formations are probably the equivalents of the Coeymans–New Scotland interval in New York, and the Fittstown Member and the upper part of the Cravatt Member are probably the equivalents of the Ross–Birdsong in Tennessee. This is of some interest because it suggests that the differences between the Birdsong and Haragan faunas may be the result of a slight difference in age rather than environment. To some extent, these ages are broadly confirmed by evidence from the unconformably overlying Frisco Formation (see following), which suggests that the Haragan–Bois d'Arc is appreciably older than the Oriskany.

Frisco Formation

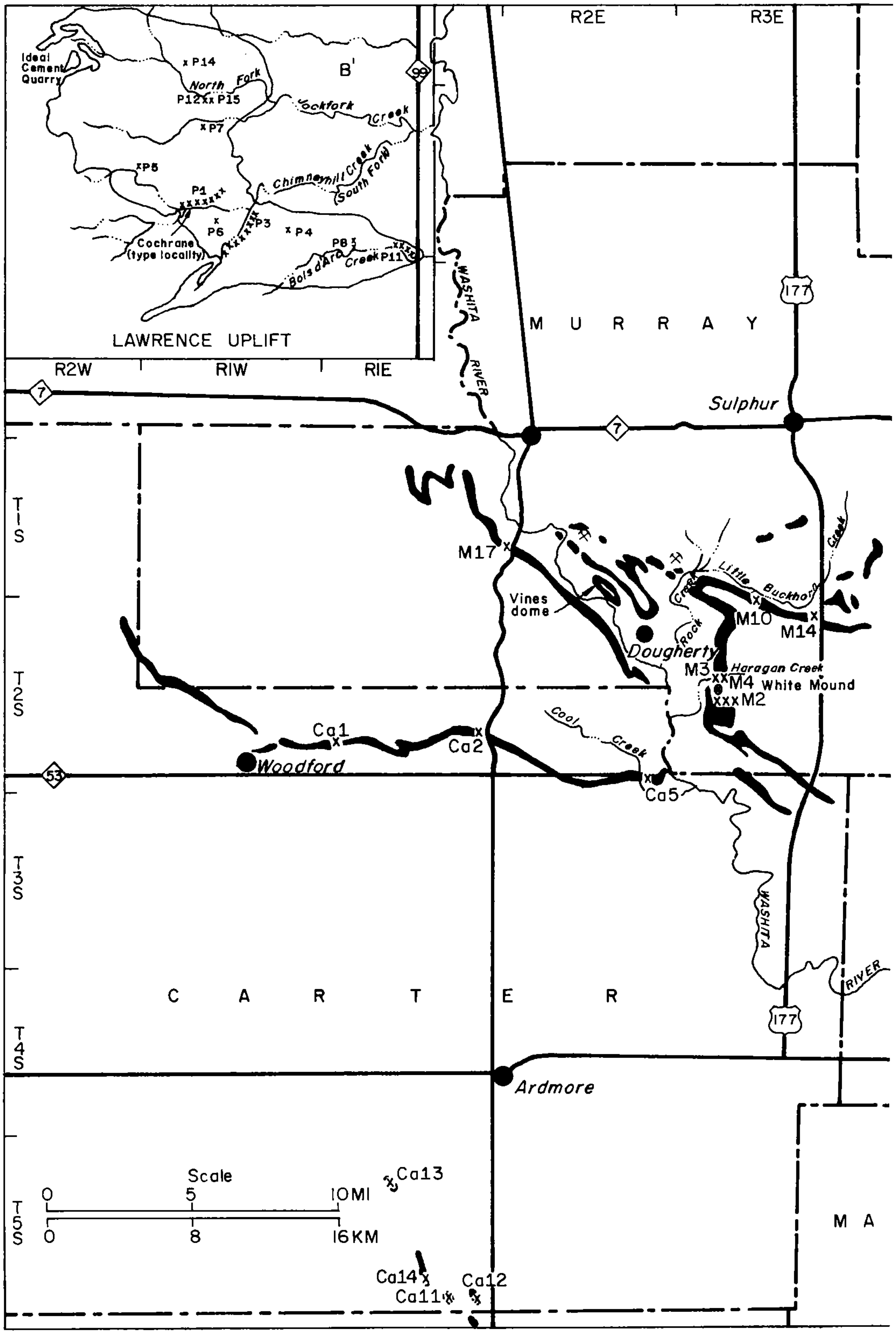
Paciphacops (Viaphacops) cristata from this formation has been compared with both *bombifrons* and *gaspensis,* which occur in the Onondaga and Grand Grève Limestones, respectively. The latter is thought to be an equivalent of the Esopus shale of New York (Lespérance and Bourque, 1971, text-fig. 2). The species *Paciphacops (Paciphacops)* sp. is closest to Eldredge's *Phacops logani* subsp. A, which is thought to come from the Becraft Limestone. The Frisco specimens are somewhat further advanced, and hence they are probably younger than the Becraft. *Terataspis* is known only from Emsian rocks in New York and Ontario, but again the specimen is too poor to make specific comparisons. *Odontochile ceraunus* is related to *O. ulrichi* Delo, the types of which occur in the Lower Devonian of Nevada. Similar species occur in rocks of Siegenian age in Kazakhstan, U.S.S.R.

None of this evidence is very precise, but it is all consistent with the Deerparkian age usually ascribed to the formation.

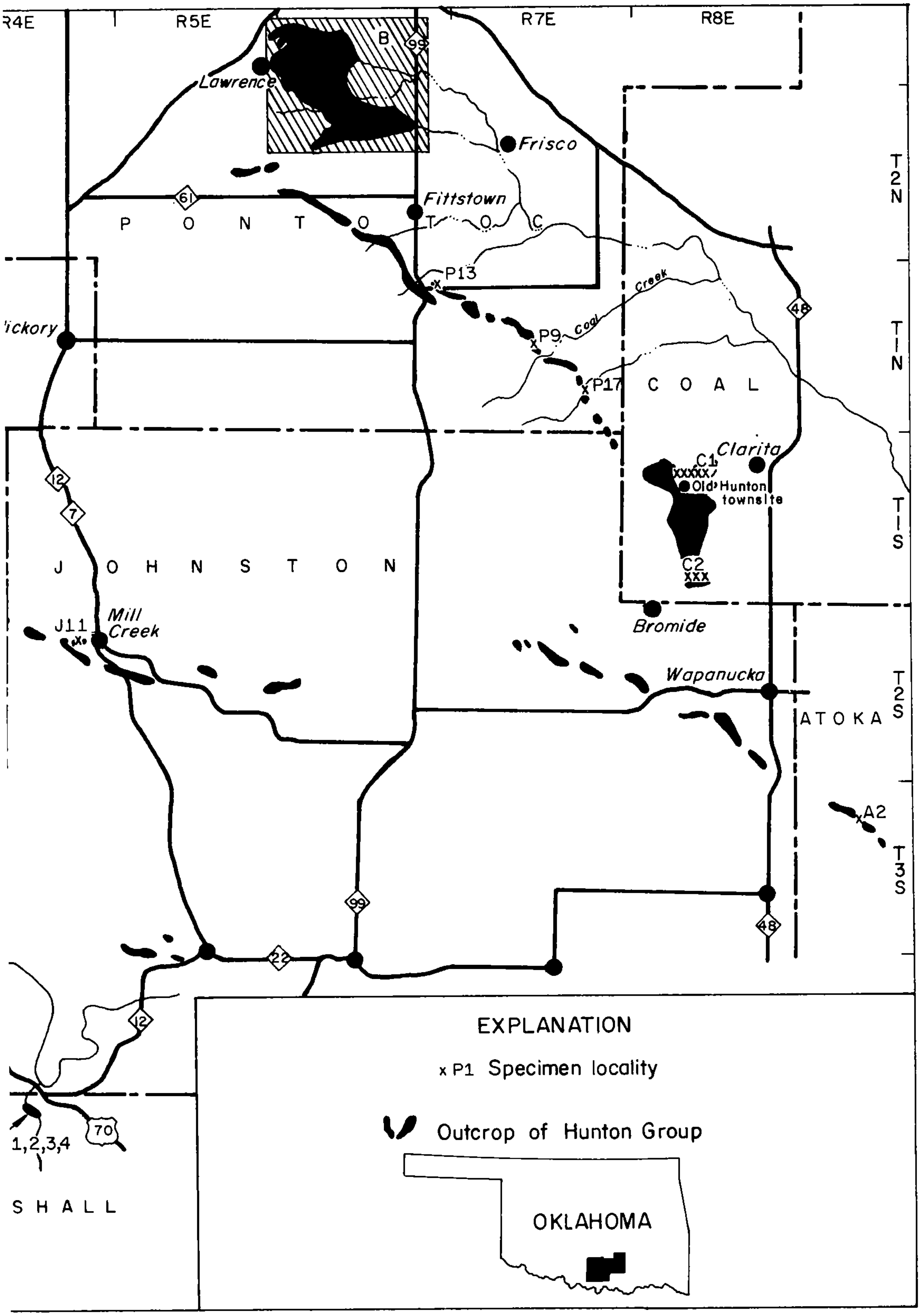
BIOGEOGRAPHY AND PALEOECOLOGY

Gedinnian

The Haragan–Bois d'Arc trilobites may be regarded as a filtered Appalachian assemblage (Ormiston, 1972) with a few endemic species. The most obvious difference from the normal assemblage is the almost complete lack of proetids, with only two specimens of Proetidae and one of Dechenellidae known from the entire collection. Another disparity is in the Dalmanitacea, with *Huntonia (Neoprobolium),* the "*Odontochile*" *pleuroptyx* group, and the coarsely ornamented Dalmanitidae so common in the Appalachian region missing from Oklahoma at this time, though some of the latter did arrive by the Emsian (Ormiston, 1968). Further, there are none of the synphoriinids which first appear in the Appalachian Gedinnian (Lespe⁶rance, 1975). On the other hand, the *Huntonia* group, so common in Oklahoma, is apparently not common in the northeastern states, although it is represented by similar species in Illinois, Missouri, Tennessee, and Mississippi, and in northern Mexico. This suggests that the group was rapidly evolving in the southwestern part of the Appalachian seaway at the same time other dalmanitaceans were evolving in the northeast. The evidence of *Phalangocephalus* suggests that some of the forms originating in the southwest later moved to the Appalachian region. Incidentally, the Chihuahua fauna described by Haas (1969) from northern Mexico probably demonstrates an extension of the Haragan



Text-figure 1. Map showing outcrop of Hunton Group in Oklahoma and localitie



om which collections have been examined. (Modified from Amsden, 1960.)

fauna farther to the southwest, the *Synphoroides biardi* of Haas now being interpreted as a representative of *Huntonia (Prosocephalus)*. This, and the associated fragmentary species, are all consistent with a Haragan–Bois d'Arc relationship.

The calymenids, Calymeninae and Homalonotinae, both of which occur in the Appalachian region, are represented by a single pygidium in the southwest. This is rather surprising in view of the fact that *Calymene* is the most abundant genus in the underlying Henryhouse Formation, which is of an almost identical facies.

Two genera, *Reedops* and *Ceratonurus,* are known from the Oklahoma faunas but have not been found in the Appalachian or any other region as early as the Gedinnian. The latter genus is represented by only two specimens, but the former is quite common. It is possible that they originated in the area.

The genera *Paciphacops, Odontochile, Otarion, Cordania, Leonaspis, Dicranurus,* and *Echinolichas* are represented by closely related species in the Oklahoma and Appalachian regions. Of these genera, *Cordania* and *Echinolichas* are not known outside the Appalachian province, but the others are cosmopolitan.

Interchange between Oklahoma and the Great Basin during the Gedinnian is improbable (Ormiston, 1972). The Gedinnian faunas in the Great Basin, however, are very poorly known. Merriam (1973) recorded some phacopids similar to *P. birdsongensis* and *P. gaspensis* from the Rabbit Hill Limestone, part of which is probably Gedinnian. Another phacopid he identified as *Phacops* cf. *P. canadensis,* also from that unit, is not similar to any Oklahoma species, but his *Leonaspis* cf. *L. tuberculata* is not too dissimilar from *L. williamsi.* The occurrence of *L. tuberculata favonia* and a species of *Reedops* close to *R. amsdeni* in the younger Wenban Limestone (Haas, 1969) also supports the idea of migration between the two regions, though it may have developed later than the Gedinnian. There is no evidence of the migration of any distinctive Cordilleran forms into the Oklahoma region either in the Gedinnian or Siegenian.

The single specimen of ?*Odontochile taffi* is of interest in that although it is unlike any described North American species, it has some similarities with European, North African, and Kazakhstanian species that have been referred to *Odontochile (Reussia)* by Maksimova (1972). Although it differs in some respects from the typical members of this subgenus, the similarities are sufficient to suggest that Old World faunas were able to gain some access, possibly by way of the Great Basin.

The pattern of trilobite distribution during the Gedinnian was similar in some respects to that of the brachiopods (Amsden, 1958; Boucot and Johnson, 1967) and in other respects to that of the ostracods (Lundin, 1971). Amsden found that most of the brachiopod genera were represented in both Appalachia and Oklahoma but that Appalachian genera had a significantly higher specific diversity. He was not able to decide whether the differences observed were the result of temporal, geographical, or environmental influences, or of all these together. The ostracod faunas of the Appalachian region are grossly different in composition from those in Oklahoma, and this is true of all Silurian and Devonian faunas studied. The critical New Scotland fauna was not considered, though the contemporaneous Dalhousie fauna of New Brunswick was. As with the brachiopods, there is a close relationship between the Haragan and the Birdsong ostracod faunas, but unlike the brachiopods the specific diversity of the ostracods is high in the Haragan. However, the Lower Devonian diversities from Lundin's table 2 show no significant differences between the two major faunal types he distinguished. Lundin believed that geographical and (or) environmental controls determined distribution of the faunas.

Putting all this information together, it seems clear that some barrier or barriers existed along the seaway between New York and Oklahoma, the most effective being between New York and Tennessee. These barriers were in the nature of filters that prevented the migration of some genera while enabling others to distribute themselves along the coast, speciating as they migrated. As Lundin indicated, conditions of temperature and salinity can produce these selective effects, and these conditions can be controlled by temporary land barriers in shallow seas.

Paleomagnetic studies show that the whole seaway from Mexico to New Brunswick was equatorial during the Early Devonian (McElhinny, 1973), and in tropical waters there are widely fluctuating temperatures governed by water depth and circulation. The Bailey, Birdsong, Haragan, Tobosa, and Chihuahua deposits all formed on broad, flat shelves covered with shallow water. Evaporation from such areas is high, with resultant high salinity gradients if circulation becomes restricted. There is some evidence from isopach maps and paleogeographic reconstructions (see Amsden and others, 1967; Collinson, 1967; McGlasson, 1967) that at least the Bailey and Haragan faunas, and those undescribed from Texas, lived in broad embayments of the northern shore of the seaway that probably were protected from the usual longshore currents but had their own local hydrographic conditions.

An alternative hypothesis is that the land bordering the southern edge of the seaway (Boucot and Johnson, 1967) continued farther to the southwest into northern Mexico. This need not have been a high topographic feature, and it may even have been slightly submerged in places. Cline (1960, p. 11) mooted the possibility of such a landmass. It is true that the Arkansas and Caballos Novaculites have been interpreted as "deep"-water depositional sites to the south of the carbonate shelves (Park and Croneis, 1969; McBride and Thomson, 1970), but this does not preclude the possibility of a southern land, provided it was of low relief. If this were so, there would have been a vast area of warm, shallow to moderately shallow water in the seaway, with limited access to the open ocean across the area under discussion. If circulation in this region were poor, warm and moderately saline water would have covered the shelves. In this connection it is important to note that in Oriskany times the seaway was constricted east of the Missouri-Tennessee outcrops by a peninsula extending down from the north (Boucot and Johnson, 1967, fig. 3a). If this land existed earlier, or even if it existed as a submerged sill, it would have affected the circulation between the southwestern and northeastern parts of the seaway. The northeast had access to the open ocean. Thus, there is some support here for the hypothesis that the hydrology of the two areas was different.

(There is a possibility that the southwest had less, rather than more, saline conditions than the northeast, particularly if it were receiving vast volumes of fresh water from rivers. This seems unlikely, however, because of the very low amount of terrigenous material in Gedinnian deposits throughout the region and the almost complete absence of coarse material reaching the areas of novaculite deposition.)

Both these hypotheses seek to explain the animal distributions in terms of increasing salinity and temperature southwest from Tennessee and Missouri, though there is no suggestion that the waters even approached a hypersaline condition. This would serve neatly to explain the decreased diversity of both brachiopods and trilobites in this direction and their generally smaller size. It may also explain the similar diversities of the ostracod faunas in the northeast and southwest, as well as their different gross faunal compositions. Recent ostracods as a group are able to cope with a much wider range of salinities than recent articulate brachiopods, and hence different ostracod groups may have been able to diversify equally in the two regions.

Siegenian

The Frisco fauna is small, but it is of considerable biogeographical importance. The new species of *P. (Paciphacops)* and *P. (Viaphacops)*, as well as *P. (Viaphacops)* cf. *bombifrons* (Hall), are typical Appalachian forms. *Terataspis* is known elsewhere only from New York and Ontario. *Otarion* is ubiquitous, and the proetids of New York are too poorly known for definite judgments about the Frisco species of ?*Proetus* to be made. If the pygidium referred to as an indeterminate dalmanitinid should prove to be related to *Corycephalus*, it would be another Appalachian representative. That leaves only *Odontochile ceraunus*, which is probably a member of the *O. ulrichi* group from Nevada; similar species occur in contemporaneous faunas in Kazakhstan. Thus, the Frisco fauna may be regarded as Appalachian with a Great Basin tinge. A similar view was reached by Ormiston (1972, fig. 1).[1]

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[1] Dr. Ormiston has informed me that figures 1 and 2 of that article were inadvertently interchanged.

Early Emsian

Ormiston (1968, 1972) interpreted the Turkey Creek fauna of this age as being the result of a temporary Bohemian incursion into the region, a judgment based in part on comparisons of *Reedops amsdeni, Ceratonurus selcanus dilatus, Proetus* cf. *P. papillaris,* and ?*Odontochile* with European species. I have attempted in this paper, however, to show that *R. amsdeni* is more closely related to older species from Oklahoma and Nevada than to Bohemian species. *Ceratonurus* and *Proetus* were established in the region by Haragan and Frisco times respectively, and the Turkey Creek forms may well have evolved from these stocks. This is not to deny the specific similarities commented upon by Ormiston, or the possible importance of the occurrence of *Cornuproetus* and *Astycoryphe,* but it should be emphasized that there is a lack of well-described Appalachian faunas of comparable age with which comparisons could be made. Little weight should be placed on the fragmentary specimen described as ?*Odontochile,* the crucial anterior border of which is unknown, nor on the specimens of *Decoroscutellum.* Scutelluids are rare in the Appalachian region, but occasional specimens keep turning up, as the present work shows, and consequently the apparent absence of *Decoroscutellum* elsewhere in the region may not be significant.

In summary, I believe that the evidence favoring the incursion of a Bohemian fauna into Oklahoma in Turkey Creek time is not as strong as it appeared to be when Ormiston reported his conclusions.

DIMORPHISM AND POLYMORPHISM

The question of differing forms in the same species is frequently discussed, but the conclusions are usually tentative and vague, the basic difficulty being failure to agree on the ground rules for recognizing the presence of a dimorphic species in a collection. The first unconsidered reaction is naturally to refer two morphs at any locality to separate species or subspecies. It should be kept in mind, however, that dimorphism is common among recent arthropods; it is, in fact, the rule rather than the exception, and many fossil arthropods as old as the Ordovician show clear sexual dimorphism. This is perhaps most obvious in the ostracods and eurypterids (Stφrmer and Kjellesvig-Waering, 1969). But trilobites display no sexual organs, and though one might expect dimorphism to be common among them its recognition must necessarily be based on secondary sexual characters that cannot be directly confirmed as such. There is also an unwillingness to accept dimorphism when a large number of characters are involved—16, for example, in the case of the phacopids discussed below. That this is not an inordinately large number is clear from an examination of living arthropods. In fact, the two morphs of the isopod *Paragnathia formica* figured by Naylor (1972, fig. 4) show differences in the proportions of all parts of the skeleton, in presence and absence of appendages and sensory structures, in size of the eyes, and in various structures of the ventral surface. Compared with these variations, the differences between the phacopid morphs pale into insignificance.

The chief criteria for recognizing conspecific dimorphs are:

1. The common occurrence in collections from one horizon and locality of two closely related but sharply distinct morphs: for example, at several Haragan localities the same two morphs occur together.
2. The common occurrence in collections from formations of similar ages of pairs of such morphs of related species, as, for example, the pairs in the Haragan, pairs of a different but related species in the Henryhouse, pairs of yet another isolated species in the Birdsong, and so on.
3. Differences between the pairs in characters that are known to be secondarily sexually dimorphic in living arthropods, such as the eyes (Clarkson, 1966, 1969) and the pygidia (Öpik, 1958).
4. The presence of three closely similar but sharply distinct morphs at any locality. Two closely similar sympatric species of a vagile benthonic invertebrate are not common in modern seas; three such species are very rare.
5. The presence at a locality of several pairs of such species belonging to totally unrelated genera is more probably the result of dimorphism than multiple sympatry. At Old Hunton Townsite, for example, there are pairs or triplets of *Leonaspis, Paciphacops, Huntonia,* and *Echinolichas.*

6. The presence at a locality of two morphs that are identical except for one strikingly different character. An example of this is the presence of an extra thoracic segment in a species of *Pagetia* (Jell, 1975).

It should be noted that frequency ratios of the two morphs are inconclusive in demonstrating sexual dimorphism rather than the presence of two species. As indicated below, frequency ratios are highly variable under differing environmental conditions.

Another problem is the apparent occurrence of trimorphism in *Paciphacops birdsongensis, Huntonia purduei,* and possibly *Leonaspis williamsi.* Trimorphism is known among living arthropods. In the Cladocera, for example, it results from the alternation of parthenogenetic and bisexual generations (Kaestner, 1968, p. 35). It is also known that some arthropods alter their reproduction patterns under certain stress conditions. The notostracan *Triops* reproduces parthenogenetically under normal conditions, but in desiccating environments males are produced as well (Kaestner, 1968, p. 97). The occasional occurrence of trimorphism among fossil arthropods is therefore not unexpected, and it may result in the above instances from the development of parthenogenetic and bisexual individuals under stress conditions for the above species.

SYSTEMATIC DESCRIPTIONS

Order PTYCHOPARIIDA Swinnerton, 1915
Suborder ILLAENINA Jaanusson, 1959
Superfamily ILLAENACEA Hawle and Corda 1847
Family SCUTELLUIDAE Richter and Richter 1955

Genus **Breviscutellum** Snajdr

Type species.—Bronteus transversus Hawle and Corda, from the Koneprusy Limestone of Bohemia.

Remarks.—The original diagnosis of Snajdr (1960) is followed.

Breviscutellum, new species

Pl. 1, fig. 7

Description.—Outline of pygidium is transverse, with length approximately two-thirds width; length of axis (without half ring) measures 0.26 of total length; anterolateral corners are broadly truncated; a line joining the points of maximum width passes through the posterior tip of the pygidium; posterior outline is broadly semi-elliptical; axis is clearly but not strongly trilobed; anterior pleural furrow is broader than all the others, straight, and directed toward the point of maximum width; more posterior furrows become increasingly concave forward, and all are of approximately the same dimensions; furrows in general are rather steep walled on their anterior edges, but by no means vertical, and are much flatter walled posteriorly, thus producing asymmetrical ribs; angle of slope of posterior wall decreases markedly from the axial to the marginal part of the furrow; surface of ribs is broadly convex. Median rib is about 3 times as wide at the margin as at its narrowest part; a faint median ridge is present on the central part of the median rib, and this ridge expands posteriorly into a triangular riblike feature bounded by prominent depressions. Ornament on the axis is of strongly arched terrace lines fading in intensity anterolaterally; pleural regions have similar terrace lines that are strongest axially and fade toward all margins, which are almost smooth; terrace lines are almost completely transverse on all ribs except the anterior pair; on anterior ribs lines swing forward at 30°-45° to a transverse line; lines number 22 per 5 mm on the median rib. Anterolaterally, the doublure extends 0.45 the distance to the axial furrow; on the outer part of the doublure, terrace lines are much finer than on the inner half.

Remarks.—This species is represented by a single, somewhat crushed pygidium. It is referred to *Breviscutellum* rather than to *Decoroscutellum* or *Kosovopeltis* because of the combination of the following characters: a transverse semi-elliptical outline, faceted anterolateral corners, the tendency of the furrows to be flat bottomed, and the asymmetrical profile of the ribs that increase in width toward the margins.

This Oklahoma specimen assigned to *Breviscutellum* is closely similar to *Decoroscutellum indefensum* Maksimova, 1968, a species which on pygidial, and probably cranidial, morphology seems to be more closely allied to *Breviscutellum* than to *Decoroscutellum*. *D. indefensum* is recorded from the Tiversk and Pribalkash (Ludlovian to Lochkovian) stages of Kazakhstan. The main difference between the Oklahoma and Kazakhstan species is in the structure of the posterior part of the median rib. The significance of this difference is not clear, as the only figured individual on which there is a subsidiary rib similar to that on the Oklahoma specimen, viz., *D. lepidum lepidum* (see Snajdr, 1960, pl. 7, fig. 4), is said to be teratological. It is possible, therefore, that the new species of *Breviscutellum* described herein and *B. indefensum* (Maksimova) are more closely related than they appear to be at first sight.

There is no described North American species that is closely comparable. The species from the Lower Devonian at Square Lake, Maine, described by Whittington (1960) as *Bojoscutellum ?pompilius* (Billings), but probably better regarded as a species of *Kosovopeltis,* has a similar broad outline, but its anterolateral corners are not so markedly truncated and its median rib is much narrower and undivided.

Material.—OU 6548 from the Fittstown Member of the Bois d'Arc Formation, Cedar Hill section, SE¼, sec. 4, T. 2 N., R 6 E., section P3-CC of Amsden, lower 7 feet.

Scutelluid, gen. and sp. undet.

Pl. 1, fig. 8

Description.—Pygidial outline is not determinable in detail, but probably is elongate; ribs, particularly the lateral ones, are slightly asymmetrical; median rib is narrow and not bifurcated; 3d to 7th ribs are progressively more curved; all ribs continue to expand in width to the periphery; axis is clearly trilobed; ornament consists of terrace lines, numbering 6-8 per mm on the median rib; doublure unknown.

Remarks.—The shape of the ribs and furrows, together with the ornament, suggests that this specimen falls into the range of morphology shown by *Kosovopeltis* and *Breviscutellum,* but it is not possible without having an entire pygidium to make a definite assignment to one of these genera.

This form is easily distinguished from the species described above and bears no close relationship to any described North American species.

Material.—OU 6820 from the Haragan Formation at section M-4, White Mound, NW¼NE¼ sec. 20, T. 2 S., R. 3 E., Murray County.

Superfamily PROETACEA Hawle and Corda 1847

Family PROETIDAE Hawle and Corda, 1847

Subfamily PROETINAE Hawle and Corda 1847

Genus **Proetus** Steininger, 1831

Subgenus **Coniproetus** Alberti, 1966

Type Species.—Proetus condensus Přibyl from the Upper Koněprusy Limestone at Měňany, Bohemia (Pragian, Lower Devonian).

Remarks.—Owens (1973, p. 10) discussed this subgenus and concluded that its originally designated type species, *P. condensus* Přibyl, is a junior subjective synonym of *P. glandiferus* Novák. He also gave a new diagnosis of the subgenus, which included data on the pygidium. Alberti's original diagnosis was based entirely on the cranidium, this being the only part of *P. condensus* that had been figured by Přibyl, although he provided a short description of the pygidium. From the figures given by Přibyl (1965) and Owens (1973) it would seem to be possible to distinguish *P. condensus* from *P. glandiferus* by the posterior position of the larger palpebral lobes and the longer anterior border of *P. condensus*. For this reason I am continuing to use the original designation of the type species.

Coniproetus sp.

Pl. 2, figs. 10, 11

Description.—Glabella is widest at the occipital ring, contracting very slightly opposite the occipital lobes, then showing a slight lateral expansion opposite the approximate position of lobe lp, beyond which it contracts slightly to the frontal lobe; anterior of glabella forms a semi-ellipse. Occipital furrow has a short, transverse medial section and anteriorly concave lateral sections and is moderately deep and well rounded; occipital ring is 0.18 times the length of the glabella (sag.), is well rounded in both lateral and longitudinal profile, and has a very faint median tubercle. Occipital lobes are subtriangular and are completely separated from the occipital ring by a furrow similar in depth to the occipital furrow; lateral glabellar furrows were not observed owing to slight decomposition of the surface but certainly could not have been well impressed; border furrow is shallow but is clearly defined and is rounded on the bottom. No preglabellar field is present; anterior border measures 0.25 times the length of the glabella (sag.), has a rather sharp posterior edge, and bears a broad, shallow depression in its surface; rostral suture is almost straight in ventral view, is broadly arched in anterior view, and is situated on the ventral surface; α is approximately on an exsa. line through the lateral end of the occipital lobe; β and γ are broadly rounded; β-β is wide and is equal to δ-δ; γ is situated just outside the axial furrow; ϵ is apparently angular and is placed at the edge of the axial furrow opposite the front tip of the occipital lobe; ω is unknown; palpebral lobe rises gently out of the axial furrow and is rather flattened on top; outline is more convex posteriorly than anteriorly. Ornament unknown.

Pygidium has a length approximately three quarters of its width; outline is evenly rounded; axis is moderately arched (tr.) and reaches to the border; border is separated from the remainder of the pleural region by a distinct furrow that fades slightly posteriorly; border is inclined at about 40° to the horizontal, is gently convex, and is narrowest at the anterolateral corners; there are 10 axial rings, each having a short, vertical lateral part but a posteriorly inclined medial part; a distinct depression on the abaxial extremity of each ring indicates site of muscle insertion; 7 or 8 pleurae are present, the posterior ones being very indistinct; pleural furrows are 2 or 3 times as strong as the interpleural, except distally, where they are approximately equal; furrows do not extend on to the border; doublure is strongly convex and is equal in width to the border. Ornament is unknown.

Dimensions.—

Length of cranidium	11.8 mm
Length of glabella	9.5 mm
Width of δ-δ	9.2 mm
Length of pygidium	6.0 mm approx.
Width of pygidium	8.5 mm approx.

Remarks.—These two specimens were collected by Amsden from the single locality named below, where they are the only proetids known. It is assumed, therefore, that they belong to the same species. The surfaces of both are slightly corroded, but it is clear that if any ornament was present, it must have been very fine.

The species is assigned to *Proetus (Coniproetus)* with some confidence. Other subgenera considered were *P. (Proetus)* and *P. (Ganinella)* Elkin, 1968, but the outline of the glabella, its flattened lateral and anterior profiles, the flattened to slightly furrowed anterior border, the small palpebral lobes, and the well-defined smooth pygidial border, all argue for *P. (Coniproetus)* rather than for *P. (Proetus)*. It should be noted, however, that the cranidial profiles, anterior border, and posterior position of ϵ on some specimens of *P. (Proetus) pluteus* Whittington and Campbell are not too dissimilar from the present species, though the pygidia of that species are quite different.

The Oklahoma cranidium is closer to that of the type specimen of *P. (Coniproetus) condensus* than to that of *P. (C.) glandiferus*, particularly in the shapes of the anterior border and the palpebral lobe. However, the glabella of *P. (C.) condensus* is a little more coniform. The Oklahoma pygidium has a somewhat narrower axis than that of *P. (C.) glandiferus*, but the overall proportions, number of rings and pleurae, border and shapes of furrows, are entirely comparable.

The Oklahoma pygidium is similar to those figured as *Ganinella batchatensis* (Chernysheva) by Elkin (1968, pl. 13, figs. 6-9). The cranidium of this form also has many features in common with the Oklahoma specimen, the main differences being in the more tapering glabella, forward position of the palpebral lobes, and coarse ornament. Owens (1973) considered *Ganinella* to be a synonym of *Lacunoporaspis* Elkin, 1968, which he regarded as a subgenus of *Proetus*. There certainly seem to be few reasons for placing *Ganinella* in the Schizoproetinae and many reasons for placing it close to *P. (Coniproetus)*, even if Owens' sweeping reassessment is not accepted.

Except for the listing of an undescribed species by Ormiston (1972, p. 603), this is the first assignment of a North American species to *P. (Coniproetus)*. It is almost impossible to work with the published illustrations and descriptions of the Early Devonian proetids from New York given by Hall and Clarke (1888), and an extensive revision is required. Dr. Ormiston has pointed out to me that one of the species Hall and Clarke figured, *P. clarus* Hall, 1861, resembles the Oklahoma specimens in size and form of the anterior cephalic border, in size and position of the palpebral lobes, and in pygidial characteristics. The Gaspé species *Proetus phocion* Billings (Clarke, 1908, pl. 9, figs. 14-16) may be a member of *P. (Coniproetus),* although it differs from the Oklahoma species in the greater size of its eyes and its short preglabellar field.

Material.—OU 6550 and 6551 from the Fittstown Member of the Bois d'Arc Formation at Cedar Hill: SE¼ sec. 4, T. 2 N., R. 6 E., P3-G6, Pontotoc County.

?**Proetus** sp. undet.

Pl. 2, fig. 1

Description.—Pygidium is 11 mm long and about 20 mm wide (estimated); axis is wide and strongly convex, in posterior view standing about twice as high as the pleurae; there are 8 axial rings plus a terminus, the 1st ring is upright but successive ones with their crests are progressively more inclined posteriorly; 1st ring is much shorter than the subsequent ones; axial furrow is slight, being represented mainly by an abrupt change in slope; axis has an almost vertical posterior; pleural regions are broadly convex; 6 pleural furrows are visible; 1st 2 interpleural furrows are almost as strong as the pleural, but more posterior ones are weaker; border is narrow and border furrow is shallow; doublure is narrow, with a flat outer and a steep inner band; doublure ornament was not observed; dorsal ornament consists of a few granules on the rings and the pleural bands.

Remarks.—This large specimen has the highly convex axis with steep posterior termination characteristic of *Proetus (Proetus).* Its other features are also found on various species ascribed to this subgenus, though its border is narrower and its pleural areas are flatter than those of the type species. It has some similarity to the *P.* aff. *P. papillaris* figured by Ormiston (1968, pl. 157, figs. 17-18) from Turkey Creek, but that specimen is much smaller and has more convex pleural areas. It is difficult to be sure of the relations with species from the northeastern states until the numerous members of the family from that region have been revised.

Material.—OU 8202 from the Frisco Formation at Payne Hollow, SW¼NE¼ sec. 22, T. 13 N., R. 23 E., Sequoyah County. Amsden collecting locality S8-C.

Family DECHENELLIDAE Přibyl, 1946

Dechenellid, gen. undet.

Remarks.—The species thus assigned is quite clearly a dechenellid, but it has not been possible to make a more positive identification. Not only does the lack of a cephalon make the situation difficult, but the characters of the pygidium exclude it from all the described genera.

The oldest known members of the family are *Paleodechenella* Maksimova, from the latest Silurian of Vaigetsch Island and Novaya Zemlya (Maksimova, 1970), and *Dechenellurus* Maksimova, which occurs as low as the Siegenian Sardzhal "Horizon" in Kazakhstan (Maksimova, 1968). The same author assigns the Emsian-Eifelian American species *Proetus latimarginalis* Hall, *P. curvimarginalis* Hall, and *P. heisone* Hall and Clarke to her genus. However, the pronounced flangelike border, the strong interpleural furrows, and the large anterior bands on the pleurae of species of *Dechenellurus* all indicate a lack of affinity with the Oklahoma specimen.

The only other genera assigned to the family and known to occur in the Lower Devonian are *Lacunoporaspis* Elkin, 1968; *Khalfinella* Elkin, 1968; *Ganinella* Elkin, 1968; *Praedechenella* Maksimova, 1952, and *Basidechenella* R. Richter, 1912. Doubt has been cast on the relationships of the first three of these by the work of Owens (1973), who considers them all to be members of the Proetinae. This opinion seems to me to be justified. The latter two genera differ from the Oklahoma specimen in having more transverse and flatter pygidia, better defined interpleural furrows, less differentiated lateral parts on the axial rings, and more sharply defined borders. In all these respects, the specimen under consideration is more similar to some of the Middle Devonian species of *Dechenella*, such as *D. para-*

granulata Ormiston. The importance of the specimen, then, is that it demonstrates the presence of the *Dechenella* lineage much earlier in the Devonian of North America than had previously been believed (cf. Ormiston, 1967).

Dechenellid, gen. and sp. undet.

Pl. 4, fig. 9

Description.—Pygidial length measures about six-sevenths of width; outline is smoothly semi-elliptical; posterior profile has a highly arched axis and pleurae flat to the fulcra, then drops steeply to the margin; total height is about half total width; lateral profile shows most of the axial crest gently inclined, but with the inclination increasing abruptly at the posterior end. Axis has 13 clearly defined rings, the front ones well rounded on the crest but the more posterior ones possibly flattened; ring furrows are deeply incised and almost straight medially, but they abruptly become shellow and deflect backward as they approach the axial furrow; a slight longitudinal furrow is present along the axis, passing through these points of deflection so that the lateral parts of the rings are clearly separated from the remainder. Most of anterior ring has a clearly defined preannulus half as long as the ring proper, a deeply incised articulating furrow, and an articulating half ring as long as the preannulus axially.

There are seven clearly defined pleurae and a large, apparently unsegmented posterior pleural region; anterior pleura is highest posteriorly, sloping into a pleural furrow with a steep anterior wall, and then onto a gently convex anterior band with an articulatory furrow in its front edge; subsequent pleurae have posterior bands and pleural furrows of similar shape, but anterior bands are almost restricted to the vertical anterior walls of the pleural furrows; interpleural furrows are present as scarcely distinguishable indentations in the fulcral regions of the first two segments only; each posterior band has a broad node at the fulcrum.

Border is narrow, steep, and poorly defined anteriorly, becoming broader, slightly convex, and more clearly defined posteriorly.

Ornament consists of anastomosing terrace lines present on the border and on at least the axial part of the anterior few rings.

Dimensions.—		
	Length of pygidium	7.1 mm
	Width of pygidium	7.7 mm

Remarks.—This single pygidium is partly corroded on the axis and on the left pleural region. For this reason the axial shapes and ornament cannot be completely described.

Material.—OU 6587 from White Mound, T. 2 S., R. 3 E., Murray County. The precise level is not known, and the small fragment of matrix attached to the specimen contains no distinctive fossils. It is probably from the Cravatt Member of the Bois d'Arc Formation.

Family OTARIONIDAE Richter and Richter 1926

Subfamily OTARIONINAE Richter and Richter, 1926

Genus **Otarion** Zenker, 1833

Type species.—*Otarion diffractum* Zenker, from the Ludlovian Kopanina Limestone of Bohemia.

Remarks.—The species described below, along with several others from the Silurian-Devonian of North America, have the cephalic features of *O. (Maurotarion)* Alberti, 1969. The main distinguishing features of this subgenus as indicated by Alberti (1969, p. 383) are the rather flat lateral profile of the cranidium, the large palpebral lobes, the divergent anterior limbs on the facial sutures, the angularly rounded anterior outline and border, and the slight lateral protrusion of lobe lp that only slightly deforms the outline of the almost parallel-sided glabella. There seems to be little difference in all these characters between, say, *Otarion elegantulum* Lovén and *O. plautum* Whittington and Campbell, on the one hand, which Alberti placed in *O. (Maurotarion)*, and *O. megalops* (McCoy), the type species of *Harpidella* McCoy, on the other, which Whittington and Campbell (1967) and Alberti (1969) regarded as a subjective synonym of *Otarion (Otarion)*. The significance of cranidial convexity should be assessed with caution, as even within *O. plautum* the range is very wide (Whittington and Campbell, 1967, pl. 7, figs. 2, 3, 12). Moreover, variations in convexity seem to have no stratigraphic or general evolutionary significance. For these reasons, and because the thorax of its type species is unknown, I have not recognized *O. (Maurotarion)* herein.

Otarion axitiosum, new species

Pl. 3, figs. 2-6

Types.—Holotype: USNM 139170 from the Haragan Formation, 3 miles west and ¼-½ mile north of Nebo, Murray County. Paratypes: OU 5284 and OU 6555 from the Haragan Formation at White Mound, NW¼NE¼ sec. 20, T. 2 S., R. 3 E., Murray County; OU 6552a-c from the Haragan Formation in sec. 19, T. 2 S., R. 3 E., Murray County; OU 6554 from the Haragan Formation about 20 feet above the bench in the middle of Amsden's C-1 section at Old Hunton Townsite.

Diagnosis.—Small; preglabellar field and anterior border each measure about one-tenth of the total cranidial length; socle is very high; furrows on posterior border overlap markedly; ornament on cranidium and inner parts of free cheeks consists of small scattered tubercles; genal spines are flattened proximally; there are 11 thoracic segments; all except last 2 thoracic axial rings have 7 small tubercles in a row near their posterior edges; pygidium has 4 rings.

Description.—Cephalic margin is highly arched medially in anterior profile and bowed down beneath the eyes in lateral profile, but the genal spine flattens out to break the smooth curve of the remainder of the cephalon; anterior outline is evenly rounded. Glabella is only moderately inflated for the genus; axial and preglabellar furrows are deep; glabella is widest opposite the middle of lobes lp; occipital ring is highest at the back, sloping forward evenly to the shallow occipital furrow; behind lobe lp, length (exsag.) of occipital ring decreases to about two-thirds its sag. length. Lobe lp reaches forward to the mid-length of the glabella; furrow 2p is indistinguishable, possibly because of poor preservation. Palpebral lobe rises steeply out of the axial furrow and turns over to become almost horizontal distally; palpebral furrow is very faint, only slightly curved, and runs the whole length of palpebral lobe; outline of lobe is well rounded; a small pit lies in the top of the palpebral area. Facial suture has δ-δ lying in front of lobes 1p, and ϵ-ϵ a little behind the middle of lobes 1p; β is well rounded and lies on the anterior border; distance β-β approximately equals δ-δ. Preglabellar field is strongly convex and is about one-tenth the cranidial length (sag.). Anterior and lateral borders are broadly rounded, approximately equal in length to the sag. length of the preglabellar field; anterior and lateral border furrows are distinctly impressed, joining in the genal angle with a short furrow running down the proximal end of the genal spine; genal spine is depressed oval in section proximally, circular distally, and extends back to the 7th or 8th thoracic segment. Posterior border furrow is in two parts: an axial part widest at the axial furrow and fading to a point behind the outer limit of the eye, and a lateral part continuous with the posterior part of the palpebral furrow. Socle is very prominent, almost as high as the visual surface itself in anterior profile, and is separated from the remainder of the cheek by an abrupt change in slope. Visual surface is unknown. Rostral suture lies just beneath the margin and is equal in width (tr.) to the glabellar width along the line δ-δ; rostral plate tapers strongly to the inner edge of the doublure but apparently is not completely triangular. Doublure is strongly convex and has a high vertical inner face beneath the lateral parts of the cheeks. Hypostome is unknown. Dorsal surface of glabella, preglabellar field, and inner parts of free cheeks have a few scattered tubercles; border has fine terrace lines around its outer edge; genal spine has similar lines on inner and outer edges and very fine granules medially.

Thorax has 11 segments. Axis tapers markedly; rings are moderately arched in anterior profile; in lateral profile they are highest at the back and slope gently forward; ring furrow is short and shallow; articulating half ring is a little longer than the ring itself. All pleurae have strong fulcral points and deep fulcral sockets that affect the pleural outlines markedly. Maximum thoracic width is at the fourth segment. Pleura on 1st segment is short and is directed obliquely backward beyond the fulcrum; it is broadly faceted and has a short pleural furrow and an acute tip; pleura on 2d segment is only a little longer lateral to the fulcrum, but the 3d segment is distinctly larger, with its extremity slightly recurved forward and its tip more obtuse; pleurae on 4th and later segments tend to become straighter, their tips are obtuse, and the pleural furrows extend almost to the extremity. First 9 rings each have 7 small tubercles in a transverse row; last 2 rings are apparently without tubercles; posterior pleural band on each segment has a small tubercle on each side of the fulcrum; remainder of segment is covered with fine granules. No axial spine is present on any segment.

Pygidium is approximately one-tenth the length of the whole animal; axis stops at the border furrow, is well rounded posteriorly, and contains 4 rings, the most posterior of which is longer than the others; 2d ring has a distinct pseudo half ring. Anterior pleural band is distinctly defined and has a pleural furrow similar in size to the first interpleural furrow; 2d pleura is much less well-defined, and the 3d is almost indistinguishable; marginal furrow is shallow, strongest axially and fading anterolaterally, possibly marking the line against which the cephalic doublure rests during enrollment. Whole dorsal surface is covered with fine granules.

Remarks.—Attention is drawn to the posterior border of the cephalon and its furrows. The existence of an inner and an outer furrow, the latter connected with the palpebral furrow, is a feature shared with some species of *Otarion* but not others. In some species, the outer furrow is connected with the lateral border furrow, but in others it is not (cf. the present species with *O. dabrowni* Chatterton, 1971). It is possible that the pattern of furrows in this area is of more than specific significance.

Attention is also drawn to the arrangement of the genal caecae on the anterior border of this species. It is remarkably similar to that figured by Alberti (1970), pl. 9, fig. 22, for *Otarion (Maurotarion)* cf. *O. (M.) novellum* (Barrande). The similarity extends even to the major trunk running from the anterolateral corner of the glabella toward β. Few other members of this subfamily showing caecae have been described or figured. One suspects that the pattern of these structures is of more than generic significance.

This new species is clearly related to *O. plautum* Whittington and Campbell, from the Late Silurian Hardwood Mountain Formation of Maine. The similarities include details of the cephalic structure and the pygidium; the thorax of *O. plautum* has not been certainly identified. Our new species can be distinguished by its larger rostral plate; by the presence of more scattered tubercles on the cranidium; by the facial suture with ω closer to the fulcrum and ϵ closer to the posterior border furrow; by the extension of the border furrow along the proximal part of the genal spine (resembling *O. instita* Whittington and Campbell); and probably by the arrangement of the tubercles on the axial rings of the thorax. This latter judgment is based on the assumption that segments assigned to Type B by Whittington and Campbell (1967, p. 465) belong to *O. (M.) plautum.* If Type A belongs to this species, there is the additional difference of a large axial spine on one of the segments.

There are obvious similarities to *O. periergum* Haas, 1969, from the Siegenian *Spinoplasia* Zone of Nevada, but that species has 14 thoracic segments, a large axial spine on the 7th segment, a more narrowly segmented pygidium, and a more anteriorly placed ϵ.

Several isolated cranidia from the Fittstown Member, represented by OU 7196D-F from Amsden collecting locality P16, are similar in proportions to this species, but they are more finely ornamented. In particular the occipital ring is finely granulate. Because of this they are referred to as *O.* cf. *O. axitiosum.* More complete material will probably require the erection of a new species.

Other material.—USNM 72564 from the Haragan Formation in Bed 6 of Matthes Section near the center of T. 1 S., R. 8 E., Atoka County.

Otarion sp. A

Pl. 2, figs. 2-9

Description.—Moderately large for the genus with largest cranidium 8.0 mm long. Glabella tapers, the anterior width being about two-fifths the occipital-ring width; front of glabella is broadly rounded, and anterolateral corners tend to be subangular. Occipital ring is about one-tenth the cranidial length medially, is highest posteriorly, and slopes gently into the shallow occipital furrow, which then rises abruptly on to the glabella. Cranidium is rather flat in lateral profile. On the interior, glabellar furrows 2p and 3p are both visible, the latter being extremely slight; on the exterior only 2p is normally visible. Preglabellar field is broadly convex and is about one-quarter the length of the cranidium. Anterior border tends to be slightly angular in outline medially, is broadly rounded in profile, and is separated from the preglabellar field by an anterior border furrow that varies from subangular to rounded in section. Palpebral lobe rises gently out of the axial furrow and then abruptly becomes flat; a broad, slight ridge runs from behind the anterolateral corner of the glabella on to the front of the palpebral lobe. Facial sutures have a line joining δ-δ passing through the anterior half of lobes 1p; distance δ-δ is approximately equal to cranidial length; β is subrounded and is situated in the border furrow; distance β-β is slightly less than δ-δ; γ is well rounded. Free cheek has a low socle; lateral and posterior border furrows join in the genal angle, sending a shallower furrow down the proximal end of the genal spine; eye was not observed; genal spine is broadbased, depressed, approximately equal in length to the remainder of the cheek, and only slightly deflected laterally from the general cephalic outline. Dorsal cephalon has no tubercles; faint terrace lines are possibly present on outer part of border and on genal spine. On internal surface, preglabellar field and free cheeks are crossed by a series of distinct caecal furrows: a large furrow runs from the anterolateral corner of the glabella toward β, and several smaller ones run forward from the preglabellar furrow; a similar furrow runs from the eye to the genal angle; between these furrows is an indistinct reticulum.

Only one thoracic segment is known; pleural furrow is deeply incised; posterior pleural band is highest at the back and slopes gently into the furrow; anterior band rises abruptly out of the furrow; axial ring is of low convexity in lateral profile; a few fine tubercles are scattered along the posterior band.

Only 1 pygidium is known; 4 axial rings are present, the last indistinct; 3 pleurae are distinguishable, the 1st having a broad, deep pleural furrow 4 or 5 times larger than the interpleural furrow; subsequent pleural furrows diminish abruptly in size.

Remarks.—This species is not well preserved, the external surfaces being particularly difficult to prepare. However, it is clear that the cephalon is essentially smooth dorsally.

It is easily distinguished from *O. axitiosum* by its smooth cephalon, proportionately longer preglabellar field, slightly angular anterior outline, and larger overall size. *O. (M.) periergum* Hass differs in being tuberculate and in having a longer anterior border, but it is similar in the form of the free cheek and genal spine.

Material.—OU 6594a-y from the Frisco Formation, southwest of St. Clair Lime Quarry, SE¼NW¼SE¼ sec. 14, T. 13 N., R. 23 E., Sequoyah County.

Family BRACHYMETOPIDAE Prantl and Přibyl, 1951

Subfamily CORDANIINAE, new subfamily

Diagnosis.—Large otarionids having a wide cephalic border with a wide epi-border furrow; genal spines are long and stout and bear the continuation of the epi-border furrow; dorsal furrows are deep, even opposite the palpebral lobes; facial suture between γ and β diverge at more than 70° to the axial line; γ and ϵ are situated well away from the dorsal furrow, and γ-ϵ is short; palpebral lobes are set at an angle to the horizontal and have a distinct furrow across the base; cephalic doublure is wide and has a variously rolled outer part; rostral plate increases in width backward; connective sutures are concave outward; tubercles on glabella and cheeks are weak to moderately strong; pits are confined to cheeks. Pygidium is large; there are 10-13 axial rings; 6-11 pleurae are present, the more posterior ones curved around behind the axis and the posterior bands tending to be suppressed; border is poorly defined but is concave overall.

Genera assigned.—*Cordania* Clarke, 1892; *Radnoria* Owens and Thomas, 1975.

Remarks.—The text had been submitted for publication when the paper by Owens and Thomas (1975) was released. Their work required complete redrafting of this section to take account of the new genus *Radnoria,* as well as to discuss their interpretation of the affinities of *Cordania* Clarke, 1892, which are very different from those presented herein. In their view *Cordania* and *Radnoria* are members of the Brachymetopinae, though the latter also has links with the Warburgellinae; these two subfamilies form the Brachymetopidae. It was, and is, my view that *Cordania* has more in common with *Australosutura* Campbell and Goldring, 1960, and *Brachymetopus* McCoy, 1847, than with *Warburgella* Reed, 1931, and in this we are in agreement. However, that is about as far as agreement extends, as I would place the Warburgellinae with the proetids and the Brachymetopinae with the otarionids, and I regard *Cordania* and its ally *Radnoria* as sufficiently distinct to warrant separation into a new subfamily.

The morphological features judged to unite the above genera (and several others discussed later) are the wide and generally concave cephalic border region, a backwardly expanding rostral plate, a large multisegmented pygidium, and absence of a preannulus on the thoracic segments. The details of these structures have been discussed by Owens and Thomas (1975, p. 817-821), but in my view some aspects of their significance have been misinterpreted. In discussing relationships there are several other characters that need to be taken into account, some of which suggest that the Brachymetopidae as they conceive it is not a natural group. These characters are:

1. The cephalic part of the dorsal furrow is deep in most of the genera in question, as it is in *Otarion;* but in *Warburgella* it is much shallower, particularly in the region of the palpebral lobes, as it is in most proetids.

2. The palpebral lobes of all the above genera except *Warburgella* are short and steeply inclined and are set off from the adjacent cheek by a distinct furrow or change in slope. This furrow is sited well out from the dorsal furrow, and the two are independent. Similar structures are normal in otarionids. In *Warburgella* the palpebral lobe is almost horizontal, and, although there is a change in ornament around its rim, there is no palpebral furrow. Such a pattern is normal in proetids.

3. The points γ and ϵ on the facial suture are close to the dorsal furrow on *Warburgella,* as in many proetids; but in *Australosutura, Brachymetopus,* and *Cordania* they are well out from the dorsal furrow, as in *Otarion.*

4. *Warburgella* has a distinct Panderian notch beneath the genal angle (Ormiston, 1971), as does *Proetus;* as far as I can determine, no such structure is present in *Brachymetopus, Australosutura,* or *Radnoria,* and it is not present in *Otarion.*

5. The shapes of the pygidial pleurae have been shown by Owens (1973, p. 5) to provide a basis for grouping proetid genera. *Cordania* and other Brachymetopinae are said by Owens and Thomas (p. 819) to have a high posterior band that "appears to be a modification of that typical of the Warburgellinae," but no justification of this statement is given. There is another character of pygidial pleurae that may be more significant: *Warburgella* has rather flat and even pleural bands that tend to become indistinct on the posterior part of the pygidium; it has no pleural bands behind the axis; and anterior and posterior bands are approximately equal throughout. This is herein termed Type A. In *Brachymetopus, Australosutura,* and *Proetides* the anterior pleural bands diminish rapidly on progressively more posterior segments, and the last few segments seem to be composed of the posterior bands only. This is herein referred to as Type B. In *Cordania* and *Radnoria triquetra* (Type C) the anterior band maintains its relative strength toward the rear, and on the last few segments it is the posterior band that reduces and withdraws from the axis. (The structure of *R. syrphetodes* is not clear.) This kind of difference is likely to be of fundamental significance in that, because new somites are added at the pygidial extremity during ontogeny, it reflects some peculiarity in somite formation.

6. The cephalic ornament pattern of *Warburgella* is distinctive, ranging from smooth to rugulose. Although *Tetinia* is smooth to granulose, *Prantlia* varies from smooth to "scaly" (Owens, 1973, p. 76). This scaly pattern has the appearance of reduced rugae. *Cordania* and *Mystrocephala* have small tubercles (granules) scattered over a background of fine pits, and *Radnoria syrphetodes* has "fine pits (on preglabellar field, cheeks, and 1 p. lobe) and granules (on glabella, anterior border, and palpebral lobe)" (Owens and Thomas, 1975, p. 816). *Brachymetopus, Australosutura,* and *Proetides* have rather larger tubercles, and, in addition, *Australosutura* has pits in the epi-border furrow. Hence *Warburgella* and *Prantlia* are considered to be allied and to be

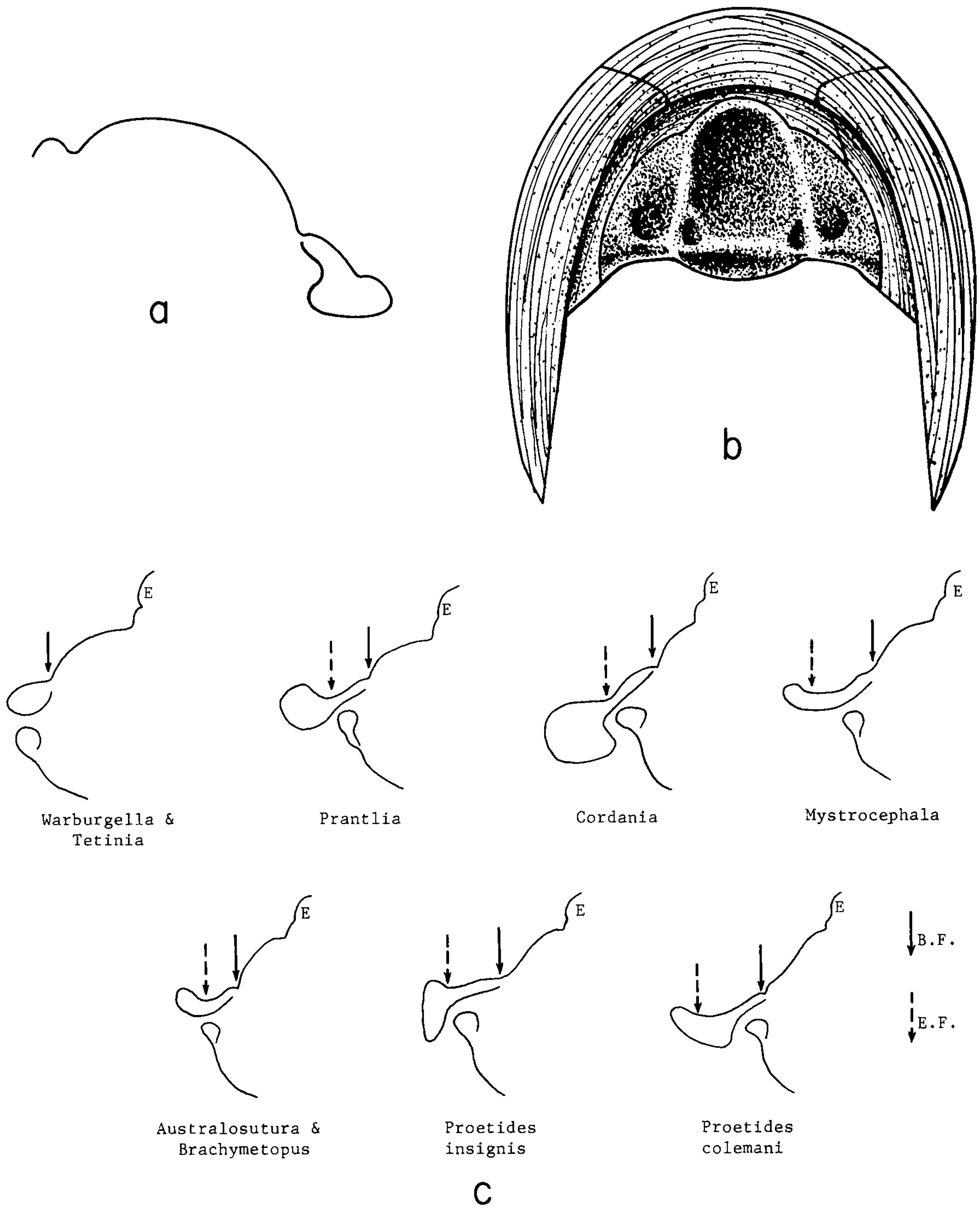
different from all the other genera.

7. Although the rostral plates of all the genera under discussion expand backward, there are several distinct types. *Brachymetopus* and *Australosutura,* in which the plate extends back to the genal region and in which the connective sutures are convex outward, clearly form one type. *Prantlia* and *Radnoria* are similar, and if only the inner part of the plate of *Cordania* is considered, as is reasonable in the light of the discussion of the border given below, it also falls into this group. It is characterized by having the hypostomal suture about equal in width to the distance between the eyes and connective sutures that are concave outward. The rostral plate of *Warburgella* has some features in common with each of the previous groups but is more like an abbreviated version of the first group.

This information, together with that provided by Owens and Thomas, suggests that the similarities in detail between *Warburgella* and the proetids are considerable, but that *Cordonia, Australosutura,* and *Brachymetopus* have just as much in common with the otarionids. Can it be then that the posteriorly expanding rostral plate, the lack of a preannulus, and the large pygidia have developed independently in a proetid and an otarionid stock? Moreover, is it likely that the otarionid stock includes two separate lineages, one leading to *Cordania* and the other to *Brachymetopus*? To examine these questions it is most convenient to list the characters of the genera under discussion. The characters listed for *Radnoria* are those of the type species except for the pygidium where *R. triquetra* has been used. But before examining this list, a problem related to the cephalic borders and doublures needs to be investigated.

Most of the genera under discussion have unusually wide cephalic borders and doublures, some of which are complex structures. Whittington (1960), Hessler (1962), and Owens and Thomas (1975), among others, consider that in such genera as *Cordania, Mystrocephala,* and *Proetides* only the relatively narrow outer convex part of the cephalon constitutes the border, and the border furrow lies directly inside this. The difficulty with this interpretation is that the doublure extends well inside the border furrow, its inner edge corresponding with a relatively minor "inner furrow" on the dorsal surface. Consequently, the doublure has to be considered as having grown inward beyond its normal position. I consider this interpretation to be mistaken. Consider the situation in *Cordania.* The thorax and pygidium are of such a size that on enrollment they lie against the *inner flattened* part of the cephalic doublure, as has already been shown by Whittington (1960, pl. 51, figs. 14-16), and as is confirmed herein. This suggests that the outer roll is not the border *sensu stricto* but a structure that has been *added* to the normal border. The faint furrow above the inner edge of the doublure is the normal border furrow. Confirmation of this is to be found in the way this furrow joins the posterior border furrow and in the way the broad "outer furrow" maintains a separate course and passes down the genal spine without deflection. This outer furrow is termed the *epi-border furrow.* All the broadly concave region lying outside the "inner" or true border furrow, together with the border roll, constitutes the true border. That part of the cranidium termed the preglabellar field by Whittington also becomes part of the border.

The situation in the other genera is best understood in terms of the enrollment relations of the cephalon and the pygidium. These are illustrated in text-figure 2c. The arrangements in *Prantlia* and *Proetides* are broadly comparable with that in *Cordania; Warburgella, Australosutura,* and *Brachymetopus* form another group; and *Mystrocephala* is probably intermediate, though the control on this reconstruction is poor and caution is necessary. The evidence of *Proetides* is important from a taxonomic point of view. It is represented by two species that have many characters in common, that are approximately of the same age, and that occur in the same area (Missouri). They differ mainly in the shape of the cephalic border and details of the pygidium. In this instance, at least, border shape is not of much taxonomic significance. *Cordania* provides a similar example. A second morph of *C. falcata,* morphologically close in other respects to the types but without the well-developed border roll, is described below. It comes from the same formation, the Haragan, as the other specimens. In the light of these data, I consider the similarities in border and doublure structure between *Prantlia, Cordania,* and *Proetides* to be due to convergent evolution.



Text-figure 2. *a*, longitudinal section of cephalon of *Cordania falcata* Whittington, showing relationship of doublure to dorsal exoskeleton.

b, ventral view of *Cordania falcata* Whittington, showing form of rostral plate.

c, schematic transverse sections through left side of cephalon and pygidium of several enrolled trilobites, taken at eye level; cephalon above and pygidium below; not all drawn to same scale; pygidial outline and doublure shape not precise. *BF*, border furrow; *EF*, eip-border furrow; *E*, eye.

Summary.—*Warburgella* and *Tetinia* are clearly allied, and despite the shape of its rostral plate and its unusually wide pygidial doublure, *Prantlia* also belongs to this group. The dorsal furrow, occipital lobes, palpebral characters, and Panderian notch leave no doubt that the group, the Warburgellinae, originated in a proetid stock.

Cordania and *Radnoria* share almost all significant characters and form a natural group here referred to the Cordaniinae.

Brachymetopus and *Australosutura* also clearly share so many detailed features that they must be classified together in the Brachymetopinae. Although some information on *Proetides* is lacking, it too most probably belongs here. *Mystrocephala,* on the other hand, is difficult to assign, as it shares characters with both the Cordaniinae and the other Brachymetopinae. It is an Early Devonian contemporary of *Cordania* and probably represents the divergent morphology from a *Radnoria*-like Silurian cordaniine to the Late Devonian–Carboniferous brachymetopines. In their dorsal furrow, palpebral characters, tuberculate ornament, wide and deep 1p furrows, and lack of occipital lobes and Panderian notches, both the Cordaniinae and Brachymetopinae betray their otarionid origin. Perhaps it is desirable to consider the erection of a Superfamily Otarionacea containing the Families Otarionidae, Aulacopleuridae, and Brachymetopidae, but this is a task for a major review.

Genus **Cordania** Clarke, 1892

Type species.—*Phaethonides cyclurus* Hall and Clarke, 1888, from the New Scotland Formation, Lower Devonian, of New York.

Diagnosis.—Glabella is strongly convex, is widest across lobes 1p, and has subangular; anterolateral corners; axial furrow is deep throughout; glabellar furrow 1p is deep and completely isolates lobe 1p; furrow 2p indents the glabellar outlines only slightly. Border furrow is slight; it joins the preglabellar furrow or passes slightly in front of it and joins the posterior border furrow well inside the genal spine posteriorly; border is very broad, with a pronounced epi-border furrow and a broadly rolled margin, both of which extend to the tip of the genal spine. Palpebral lobe is high and is situated with δ-δ across the anterior parts of lobes 1p. Facial suture is widely divergent (at about 90° to the midline) in front of the eyes, and with ω just inside the base of the genal spiines. Rostral suture lies just on the ventral surface of the margin. Doublure is broadly convex beneath the outer part of the border, is reflexed on itself beneath the epi-border furrow, and then becomes closely appressed beneath the inner part of the border. Rostral plate contracts back from the margin and then widens posteriorly. Glabella, the outer part of the border, and to a lesser extent the inner part of the border are tuberculate; cheeks inside the epi-border furrow have numerous pits. Thorax has nine segments, anterior ones with pointed pleural tips but the posterior ones almost quadrate; tips of the pleurae lie well above the base level of the genal spines. Pygidium is almost semicircular in outline; posterior profile of both axis and pleurae is high; border is concave and has a slight convex rim; there are about 10 complete axial rings plus 1 or 2 incomplete; 8 to 10 pleurae are present, the most posterior ones being slightly convergent onto the post-axial region; on the more posterior pleurae, the posterior band fails to reach the dorsal furrow; there are fine perforations through the margin of the exoskeleton. Thoracic and pygidial rings and pleurae have weak tubercles.

Range.—*Cordania* is known definitely only from the Appalachian province, between Gaspé and Oklahoma. It has been doubtfully reported also from Lower Devonian rocks in Morocco (Alberti, 1969, p. 290), but the single specimen reported is a pygidium with too large and too well-defined an axis, too few axial rings, no border rim, and pleurae that are too narrow between the fulcra to permit an assignment to *Cordania.* It does not even appear to be related to the Cordaniinae.

Cordania falcata Whittington, 1960

Pl. 4, figs. 1, 2; pl. 5, figs. 1-4

Cordania falcata WHITTINGTON, 1960, p. 411-2, pl. 51, figs. 8, 11, 14-18, pl. 52, figs. 3, 5.

Description.—This description is intended to complement that given by Whittington (1960, p. 411).

The glabella tends to have subangular anterolateral corners. On well-preserved specimens the faint furrow of 2p can be clearly seen on the flanks of the glabella, and in front of it there is a faint pit in the dorsal furrow, probably corresponding with 3p. Right in the anterolateral corner there is a yet fainter depression that may represent the antennulary pit. Rising out of the dorsal furrow opposite furrow 2p is a slight ridge that runs posterolaterally across the outer edge of the palpebral area. Outside it the palpebral furrow is indistinct. The palpebral lobe is steeply inclined, though it flattens out slightly toward δ. The outline of the lobe is distinctly asymmetrical, with a gentle curve in front of δ and a sharp one behind. There is a slight pit in the distal part of the lobe. The course of the facial suture is clearly shown on the plates, but note that the rostral suture is on the ventral surface about 0.5 mm behind the anterior margin and parallel to it. The eye is not globose, its height in standard orientation being only a little less than its length. There is no socle, the base of the visual surface being formed of a slight furrow below which the cheek slopes away in an even curve.

The epi-border furrow is strong and runs around the entire cephalon from the tips of the genal spines. The border furrow is weaker but is always obvious nevertheless. It is formed mainly by a change in slope of the surface. The posterior border furrow meets the lateral one in the genal region, and there is no connection with the epi-border furrow. This means that the genal spine is formed of the backward extension of the posterior border above and the extension of the lateral border roll below. These two are separated by the epi-border furrow on the external face of the spine and a matching furrow on the inner face, producing a complex structure as shown in text-figure 2.

The cephalic ornament is distinctive. The top of the glabella is covered with irregularly arranged tubercles that do not extend far down the flanks of the glabella. Lobe 1p has a few tubercles on the crest. On the occipital ring there is a transverse row of five tubercles, the largest in the middle, with the two on each flank progressively smaller. The dorsal surface of the border also bears tubercles, usually, but not invariably, largest and densest in front where they are high and conical. The border roll has tubercles along almost its entire length; these tubercles fade toward the ends of the genal spines. The size of the spines on this roll varies systematically: the coarser spines are on the top of the roll, and they decrease toward the margin, where there is a matrix of granules between them. Although the tubercles on the posterior border number only one or two and are very weak, those on the continuation of the border down the genal spine are numerous and larger. The tubercles are very sparse on the free cheek below the eye. There are no tubercles in the epi-border furrow.

The cheeks also have a reticulum formed by irregularly arranged pits. These are normally much smaller in size than the associated tubercles, but on weathering they seem to be selectively enlarged. The coarsest pits lie on the cheeks between the border and epi-border furrows, and this band of them extends back along the genal spine. Beneath the eye and on the border roll, the pits are of comparable sizes.

The doublure is in three parts. Around the outside is a gently convex, horizontally disposed band that is about 0.5 mm wider than the dorsal surface of the border roll; this band is covered with coarse terrace lines numbering four per mm. Inside this band there is a steep and forwardly reflexed median band that throws the doublure forward against the inner edge of the epi-border furrow, almost isolating the border roll. This part of the doublure is smooth or is crossed by very faint irregular medial ridges, especially in front. The inner doublure band lies against the inner part of the dorsal border, leaving only a narrow space between them, with its inner edge lying just inside the border furrow. The surface has much finer terrace lines than the outer band, and it has the same irregular ridges as the median band. I assume these to be the sites of the caecal system.

The hypostomal suture, if there is a calcified hypostome, lies parallel to the edge of the preglabellar furrow.

The thoracic segments are equal in length. The widest axial ring is usually on segment 3 or segment 4, and there is a decrease in axial width from there to the last segment, the ring of which is always narrower than that of the first segment. The pleural furrow is straight and begins behind the anterolateral corner of the ring, so that the two pleural bands tend to be of approximately uniform length (exsag.) throughout their width. The posterior band is slightly but distinctly the larger. The pleural tips on the first segments are acute and have broad facets behind which the posterior bands taper abruptly. Successive pleural tips become progressively less acute, and the last one is truncated almost at right angles. On all segments the pleural furrow terminates rather abruptly lateral to the fulcrum. Each axial ring has a small median tubercle and two on each flank, the outermost one being very faint. This makes five on each ring, and they are in line on successive segments and the occipital ring. On the posterior pleural band there is a pair of small tubercles, one at the fulcrum and another about halfway to the dorsal furrow. These also are in line on successive segments.

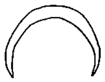
The pygidium is just about semicircular in outline. In lateral profile it is highly convex along the axis but concave post-axially. The axis has 9 or 10 distinct rings and 1 or 2 indistinct ones plus a tiny terminus. The dorsal furrow is almost indistinguishable as it turns around the end of the axis. In posterior profile the axial rings tend to be parabolic. Just above the dorsal furrow, the first seven rings have small, smooth, crescentic excavations in their front edges, presumably for muscle insertion. Nine or 10 pleural furrows are visible, the last ones swinging around behind the axis. The border is indistinctly defined by a slight break in the slope of the pleural bands over the inner edge of the doublure. A narrow, convex border rim is present. The anterior pleural furrows are straight and strong, but the posterior ones are progressively more curved. The interpleural furrows are also strong, and they follow the shapes of the pleural furrows. The posterior pleural bands are strong and reach right to the margin; the anterior bands are weaker and terminate inside the border rim. The eighth and subsequent posterior bands do not reach the dorsal furrow. The ornament of the rings consists of a median tubercle and 4 or 5 smaller tubercles on each flank. There is a row of 4 or 5 similar tubercles on each posterior pleural band. Extremely fine granules are present, but they are usually removed during preparation so that their extent is unknown. The doublure is convex beneath the rim, but its inner band is very steep. It is ornamented with terrace lines comparable in size with those on the inner cephalic doublure.

Material.—OU 3635, OU 5243-47, OU 6541, OU 7193-4, from the Haragan Formation at Old Hunton Townsite, Amsden collecting locality C1, levels H to O, NW¼ sec. 8, T. 1 S., R. 8 E., Coal County. OU 6541, Haragan Formation in sec. 19, T. 2 S., R. 3 E., Murray County. USNM 139167-8 from the Haragan Formation at White Mound, NW¼NE¼ sec. 20, T. 2 S., R. 3 E., Murray County. OU 5248 Haragan Formation, NW¼NE¼ sec. 20, T. 2 S., R. 2 E., Amsden collecting locality M1-L (surface), Murray County.

Description of Type B.—Three specimens, all purchased from Geological Enterprises, Ardmore, Oklahoma, and stated to come from the Haragan Formation at "Clarita, Coal Co., Okla.," belong to a different group. The locality given is presumably the Old Hunton Townsite, and the material is in a Haragan lithology.

Each specimen has an almost whole pygidium, and most of the thorax and cephalon, though the surfaces, especially of the thorax and pygidium, have been heavily abraded. They all seem to be similar to the type material of *C. falcata* except in the structure of the anterior border. The epi-border furrow is either not developed or there is a faint furrow just inside the margin separating off a narrow convex edge; hence there is no anterior border roll, and the furrow running down the genal spine is connected with the border furrow *sensu stricto*. The border slopes evenly down from the border furrow. On one specimen the front of the cephalon is missing. On the second the border furrow meets the preglabellar furrow in the usual way for the species, but on the others it passes well in front of the preglabellar furrow, leaving a tuberculate preglabellar field between (see pl. 5, fig. 4). The tubercles on the border are not as large as those on normal specimens, and they are more closely spaced. The doublure has a normal shape, but the reflexed band lies against an undifferentiated part of the border. There is a possibility that there are more weak tubercles on the occipital ring and the thoracic rings. As many as seven of these, in two rows and alternate in position, can be counted on one flank of one thoracic segment, but it is not known if this is the norm.

Table 1.—Morphological Characteristics of Genera of the Brachymetopinae, Cordaniinae, and Warburgellinae

		GENUS	Dorsal furrow	Glabellar shape	Furrow 2p	Occipital lobes	Borders	Tropidium	Palpebral lobe shape	Palpebral furrow	β - γ	Rostral plate	Panderian notch	Cephalic ornament	Preannulus	Pygidial terminus
	Warburgellinae	Warburgella	Shallow	Fiddle-shaped	Moderate	Present	Narrow convex	Present	Long	Absent	30°-40°		Present	Smooth to rugulose	Absent	Type A
		Tetinia	Shallow	Fiddle-shaped	Moderate	Present	Narrow convex	Absent	Long	Absent	30°-40°	?	Present	Smooth to granulose	Absent	Type A
		Prantlia	Shallow	Fiddle-shaped	Moderate	Present	Wide with epi-border furrow	Absent	Long	Absent	35°-40°		?	Smooth to scaly	Absent	Type A
Brachymetopidae	Cordaniinae	Cordania	Deep	Tapered	Weak	Absent	Wide with epi-border furrow	Absent	Short	Present	70°-75°		Absent	Tuberculose + pits	Absent	Type B
		Radnoria	Deep	Tapered	Weak	Absent	Wide with epi-border furrow	Absent	Short	Present	70°-75°		Absent	Smooth or granulose + pits	Absent	Type B
	Brachymetopinae	Mystrocephala	Deep	Fiddle-shaped	Strong	Absent	Wide with epi-border furrow	Absent	Short	Present	70°-75°	?	Absent	Tuberculose + pits	Absent	Type C
		Brachymetopus	Deep	Tapered	Weak	Absent	Narrow with epi-border furrow	Absent	Short	Present	-		Absent	Tuberculose	Absent	Type C
		Australosutura	Deep	Tapered	Strong	Absent	Narrow with epi-border furrow	Absent	Short	Present	30°-40°		Absent	Tuberculose + pits	Absent	Type C
		Proetides	Deep	Tapered	Moderate	Absent	Wide with epi-border furrow	Absent	Moderate	? Present	30°-40°	?	Absent	Tuberculose	Absent	Type C

Remarks.—The meaning of these specimens is not clear. They certainly belong to *Cordania,* as the whole basic structure, the ornament, and the reflexed doublures show. Further, in all features except the border structure, they are indistinguishable from *Cordania falcata,* but there are no specimens intermediate in border structure between them and the normal type. They probably occur at the same locality as normal specimens. Dimorphism is a possible explanation.

Material.—ANU 14849, ANU 21005 and ANU 21027, from the Haragan Formation, Clarita, Coal County (probably Old Hunton Townsite).

Order PHACOPIDA Salter, 1864
Suborder PHACOPINA Struve, 1959
Superfamily PHACOPACEA Hawle and Corda 1847
Family PHACOPIDAE Hawle and Corda, 1847
Subfamily PHACOPINAE Hawle and Corda 1847

Remarks.—Since my review of the main genera in this subfamily published in 1967, there have been several contributions that require comment. These include the works of G. K. B. Alberti (1969, 1970), Přibyl and Vaněk (1970), Chlupáč (1971, 1972), Eldredge (1971, 1972, 1973), Eldredge and Gould (1972), Maksimova (1972), and Struve (1972). Most of the new genera and subgenera erected by these workers have been based on groups of species with one or more common characteristics, and there has been no explicit philosophy behind their establishment. Eldredge (1973, p. 334), on the other hand, erected no taxa above the species level and enjoined other workers not to split the subfamily further until its evolution is more fully understood. He advocated a modified cladistic approach (Hennig, 1966) to the problem of the definition of genera and higher taxa. This should result in "vertical" groupings based on kinship, which is defined in terms of recency of common origin. For reasons that have been set out in detail elsewhere (Campbell, 1975) I am unable to accept this approach.

In my previous work, I have attempted to show that within the subfamily Phacopinae there are species groups that fall into two categories. Those in the first category are recognized by a number of distinctive characters that could be formally derived from stratigraphically older groups, but which apparently became extinct without being transformed into subsequent morphologies. These species groups were given generic status —for example, *Reedops, Eophacops,* and *Phacopidella.* In addition to these groups, there appeared to be a main "trunk" of the phylogenetic tree within which one could recognize a number of evolutionary trends (morphoclines with a time orientation) but within which the skein of transformation was so entangled that it was not possible to recognize the separate strands. For this reason, the trunk was divided into horizontal groups defined in terms of the stage reached on the specified character trends. The genera recognized in this way were *Acernaspis, Ananaspis,* an unnamed genus based on *"Phacops" logani,* and *Phacops* s.s. According to the cladistic approach, this procedure is not acceptable, because it obviously results in paraphyletic and polyphyletic taxa.

It is necessary, therefore, to reexamine the bases on which my arguments were founded. Naturally, some of the reasons for this approach are diametrically opposed to cladist principles; and it must be admitted that not all of them can be completely justified. Some have been tested by years of paleontological experience; others are more in the nature of statements of faith about the nature of the fossil record (compare Eldredge and Gould, 1972, p. 98). They are set out below.

1. Stratigraphy presents primary data for the ordering of morphological data into evolutionary patterns. No circularity of argument is involved in this statement. Stratigraphic correlation does *not* depend on knowing the evolutionary sequence. Evolution provides the variety of organisms which are then ordered by means of observed (not inferred) stratigraphic superposition. Only after superpositional ordering has been carried out with several groups of organisms in several places is it possible to produce evolutionary patterns with confidence. Most of the basic work on correlation necessary for evolutionary studies has been done. Current disputes on correlation involve time inter-

vals so short that they are likely to affect evolutionary studies at the species level only.

2. It is impossible at the present stage of knowledge to prepare extensive phylogenetic diagrams *at the species level* for most groups of fossil organisms in the Paleozoic, and because the record is too poor, it will probably always remain so. There is always the possibility that such diagrams could be prepared for certain groups of organisms for limited periods of time, but for most groups of benthonic marine organisms, and for all terrestrial ones, the range of such possibilities is negligible. The best that can be done is to indicate that a morphology of a certain type, usually represented by a generic or subgeneric name, was derived from another similarly represented morphology.

3. If all the known *species* of comparable morphology (a sufficiently vague phrase that does not imply prior knowledge of higher taxa at the initial stage of an analysis) are set out with their known time ranges, it will be seen that at any given time there are structures that can be transformed into younger ones, and others that cannot be so transformed. The former define the ongoing parts of a phylogenetic diagram; the latter define the terminal lateral branches. This simple approach is open to the criticism that snippets of the history of a lineage discovered in the fossil record may give an erroneous idea of the time of origin of a morphological type, as well as its source. It is also open to the criticism that errors of judgment can easily be made about the possibility of deriving one structure from another. However, it does take into account pieces of information that have to be explained but that are conveniently ignored by the cladists, and the errors of judgment are not likely to be worse than those involved in recognizing apomorphic characters.

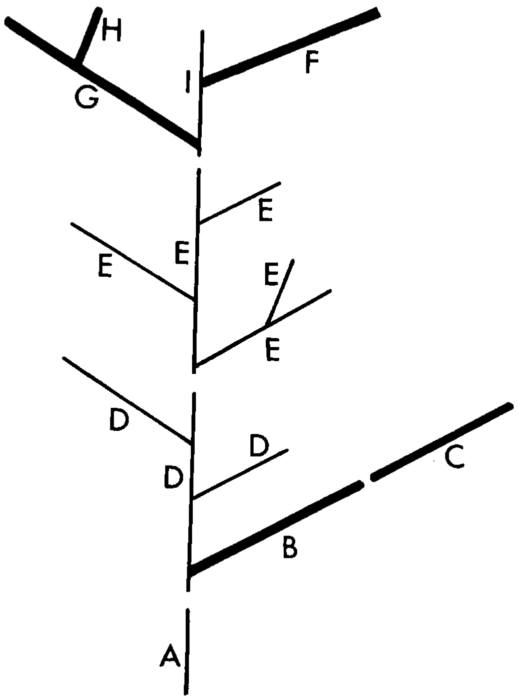
An example of the method is found in the recognition of the *Eophacops* lineage discussed below. In a distribution diagram of Silurian phacopoid species there is a small group (*handwerki, trapeziceps, musheni,* etc.) characterized by the depressed glabellar profile, strong 3p glabellar furrows, large eyes, weak ornament overall, and poorly defined furrows in the pygidium. Existing with this is another group (*stokesi, communis,* etc., which I have referred to the genus *Ananaspis*) with a swollen glabella, weak 3p furrows, large eyes, and moderately strong tubercular ornament with a cover of granules. Both these morphologies could theoretically be derived from the preexisting *orestes* type of morphology. The *Ananaspis* morphology can be readily transformed into that associated with *P. logani,* which in turn can be transformed into the *P. cristata* morphology, and so on. However, the *Eophacops* morphology cannot be transformed into any known later morphology without a prior reversion. Hence, it defines a side branch from the main stock.

4. Parallel evolution will affect the results of this method as much as any other method. Its certain detection at the genus level is rarely possible, and in most cases in which it is said to have been detected in Paleozoic invertebrates there are alternative explanations. Classifications that involve the recognition of extensive parallelisms at the generic level are inherently unstable and should be avoided.

5. It follows that polyphyletic and paraphyletic genera are inevitable in most groups. The force of this apparently defeatist conclusion is somewhat mitigated by the observation that the geological and biological returns from most of the very time-and-energy-consuming attempts to recognize monophyletic genera are negligible, even if the attempt can be considered successful (see Bulman, 1969).

As a consequence of these considerations, one envisages the subdivision of a hypothetical sequence to be as shown in text-figure 3, where the letters refer to groups of species with comparable morphologies. The branches represented by thick lines (B, C, F, G, H) are identifiable side branches and hence are recognized by a separate name, or by two names, where morphological transformation on a sufficient scale has taken place. The side branches represented by the thin lines (D, E, I) are not distinguishable from the trunk, and hence are given the same designations.

With particular reference to the phacopids, it is interesting to note that there is agreement between Eldredge and myself on the existence and nature of chronoclines in the group from the Early Silurian to the Middle Devonian. This leaves the definition of horizontal genera a matter only of deciding upon convenient boundaries. Because the chronoclines are defined by reference to *independent* time controls, genera defined in



Text-figure 3. Hypothetical phylogenetic diagram showing relationships mentioned in text.

this way are of real time-stratigraphic value. Also, as the definition of neither the "terminal branch" nor the "trunk" taxa have inbuilt *geographic* characteristics, they can be used for studies of global biogeography. It should be noted, however, that provinces defined on the basis of such genera will be of maximum extent, as they will be broadened by the failure to recognize parallelism in well-separated areas.

Recently erected Early Devonian genus-group taxa

It is now necessary to examine the genera and subgenera proposed by other workers. As mentioned previously, there is no explicit philosophy behind any of them, and the main objectives of the subsequent discussions are to determine (a) if they are worthy of recognition; (b) if so, how they are to be recognized; and (c) how they fit the evolutionary pattern of the subfamily.

Chlupáč (1971, 1972) has restricted my definition of *Phacops* to the subgenus *Phacops* (*Phacops*), and he has erected several new subgenera: *P.* (*Prokops*), with type species *P.* (*Prokops*) *prokopi* Chlupáč from the Pragian Dvorce-Prokop Limestones; *P.* (*Chotecops*), with type species *P.* (*Chotecops*) *auspex* Chlupáč from the Eifelian Choteč Limestones; and *P.* (*Boeckops*), with type species *Phacops boecki* Hawle and Corda from the Pragian. In addition, a new genus *Lochkovella*, based on *Phacops miser* Barrande, was proposed. Chlupáč's proposals are now discussed:

1. *Phacops* (*Prokops*), which is monotypic, is known only from the late Pragian in Bohemia. It has undergone reduction of external ornament to patchy granulation; lobe and furrow 1p are well developed; the eye has a forward position and has only 7 to 9 files in which the lenses are irregularly reduced in number to 25-30; the pygidium is short, and both the axial rings and the pleural and interpleural furrows are reduced in size and number. Comparison with the type species of *Reedops*, *R. bronni* (Barrande), which also comes from the late Pragian of Bohemia, shows that it has most of these features, and the glabellar shape seems to be almost identical; but the eye morphology is different. There are no other species of *Reedops* with eyes as reduced as those of *P.* (*Prokops*). Chlupáč dismisses *Reedops* in his comparison because it differs in the "discontinuous vincular furrow and in the configuration of the eyes." As has been noted elsewhere, the presence or absence of a slight vincular furrow anteriorly is not of much consequence functionally or taxonomically. There seems to be no reason, therefore, to place this form with *Phacops* rather than *Reedops*, and it could be regarded as an aberrant species of *Reedops* rather than as a separate subgenus. If other similar forms become known, subgeneric status could be accorded to the group.

2. *Phacops* (*Chotecops*) was conceived in much broader terms and includes species ranging geographically from the Urals to the Harz Mountains and from England to North Africa, and having a time range from the late Early Devonian to the Late Devonian. According to Chlupáč (1971, p. 259), this subgenus is intended to embrace the *breviceps*

group of *Phacops*. *P.* (*Chotecops*) is well advanced along most of the trends exhibited by the subfamily. The glabella is drawn out anterolaterally; glabellar furrow 1p is strong and lobe 1p is isolated; lobes 2p and 3p are indistinct; the ornament of the cephalic doublure consists of terrace lines; the hypostome is elongated posteriorly and has the three posterior spines as in *Phacops* s.s.; the thoracic axial rings are not notched at their distal ends; and the interpleural furrows on the pygidium are weak. There are several features that are not consistent with the trends leading to *Phacops* s.s. These are the reduction in the size of the ornament on the dorsal surface; the weakness of the axial furrows on cephalon, thorax, and pygidium; the posterior convexity of the hypostomal suture, the reduction of the pygidial pleural furrows; and the shortening of the pygidial axis and reduction in the number of axial rings. These characters can be regarded as defining a group that has split off from the main lineage leading to *Phacops* s.s.

It is apparent, both from the transverse nature of the ornament on the front of the glabella (in this respect, resembling *Phacops* s.s.), and from the size of the ornament elsewhere on the glabella, that the "pustules" are reduced tubercles rather than the remnant of a granulation that covered previously existing tubercles. This suggests that the *P.* (*Chotecops*) group was derived from the main *Phacops* lineage after the loss of overall granulation, i.e., in late Siegenian time or later. The hypostome, glabellar shape, and doublure ornament indicate divergence in late Emsian times or later, but the hypostomal sutural shape suggests divergence no later than Emsian. It is not surprising, therefore, to find that the first known member of the group that can be called characteristic is Eifelian in age, but that *Phacops corallinus* Richter and Richter and *P. corallinus successor* Haas, 1968, from the Emsian of Turkey are also possible members. They would be ideal transitional forms.

I have not checked all the species assigned to *P.* (*Chotecops*) by Chlupáč, nor have I examined the group in detail with regard to the recognition of possible trends. However, no species named *speculator* was described by Meischner (1965). *Phacops speculator* Alberti, 1970, from the Eifelian of Morocco, apparently belongs to *Phacops* s.s., and *Nephranops spectabilis* Meischner, 1965, is, in my opinion, best assigned to *Struveaspis*.

Some comment on the relationship of the group to *Reedops* is necessary, because Chlupáč has made the comparison and there is a superficial similarity in ornament. Is there a possibility that it has developed from *Reedops* rather than from the *Phacops* s.s. lineage? This is most unlikely, because the glabellar profiles and the shape of the anterolateral corners of the glabella are typical of late Emsian-Eifelian *Phacops* s.s. but bear little relation to those of *Reedops* species of the same age. Supporting information comes from the deep, continuous vincular furrow and the weakly notched thoracic axial rings, which are not similar to those of *Reedops*.

The group contains several species, is widespread through Europe and Asia, ranges over a long span of time, and forms a separate lineage. It should be accorded a rank similar to that of *Reedops*, and I therefore treat it as a full genus.

3. *Phacops* (*Boeckops*) Chlupáč, 1972, was intended to encompass a group of species around the type, *P.* (*Boeckops*) *boecki* Hawle and Corda. Most workers in recent times have placed the group in *Reedops*, but Chlupáč, emphasizing the continuous vincular furrow, assessed its relationship to be with *Phacops*. It differs from both *Phacops* s.s. and *Reedops* in its much reduced glabellar lobe 1p and its abbreviated pygidium. It is difficult to know if all the species mentioned by Chlupáč (1972, p. 398) form a natural group, either vertical or horizontal, because vital pieces of information are missing for some; for example, the pygidium of *P.* (*Boeckops*) *proponticus* Haas is unknown. However, the eye morphology, the low angle (50°-60°) of divergence of the axial furrows in front of 1p, and the sparse pustulose ornament are rather uniform in all the species, and this tends to confirm his assessment. The affinities of the group do seem to be with the *Phacops* line rather than with *Reedops* for the following reasons: the glabellar ornament is coarser than *Reedops;* the ornament of the doublure has begun to coalesce to form marked linear patterns, a feature that is normal in members of the *Phacops* s.s. lineage but that is not so clearly expressed in even the most advanced species of *Reedops* [compare *P.* (Boeckops) *delphinoides,* Chlupáč, 1972, pl. 3, fig. 4, with *Reedops modestus* (Barrande) and *R. schmidti* (Eichenberg) in H. Alberti, 1965, pl. 4, figs.

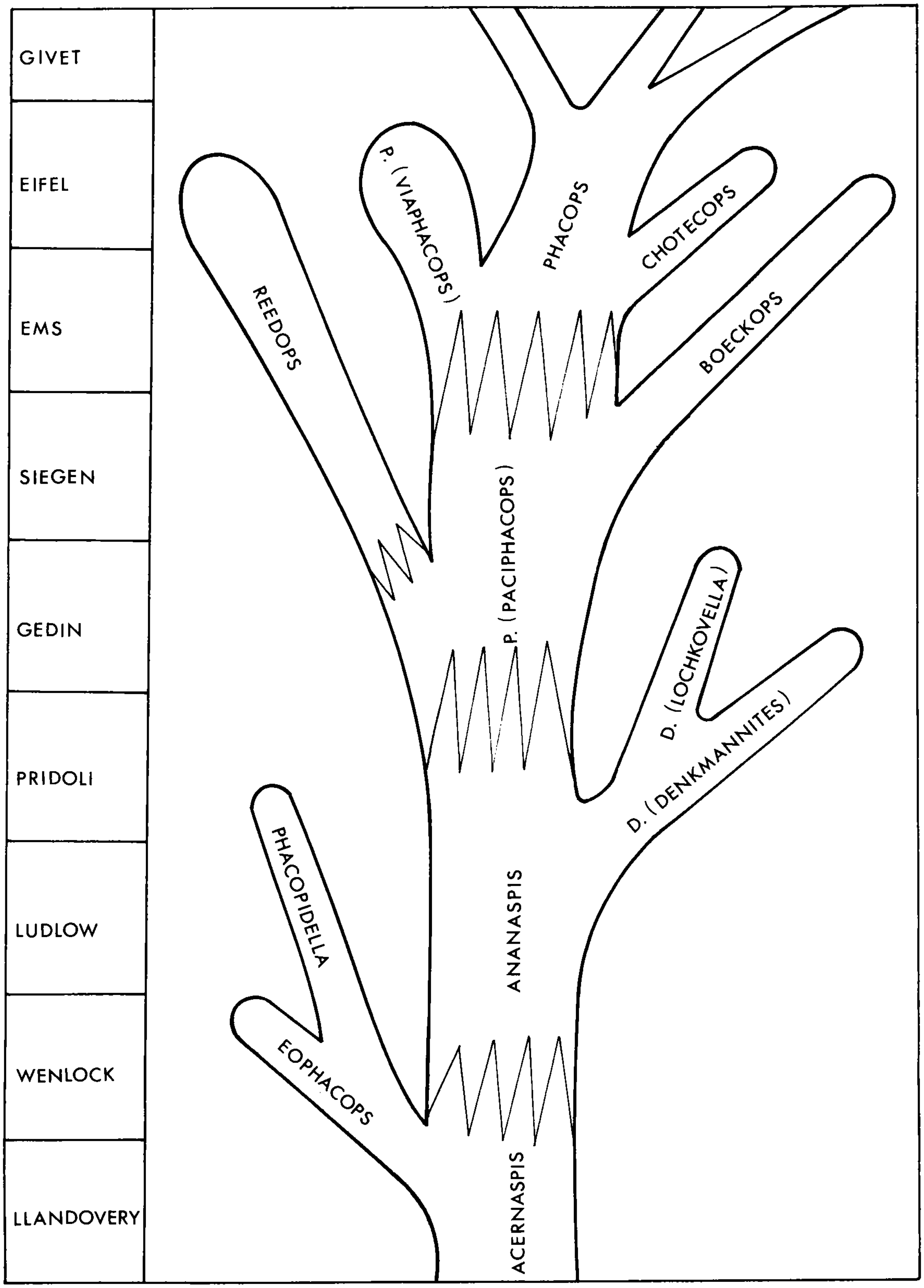
7a and 8b]; the anterior part of the vincular furrow is much stronger than is normal in *Reedops,* and the shape of the pygidial margin in both *P.* (*B.*) *boecki* and *P.* (*B.*) *delphinoides* indicates that it fitted into the edge of the furrow rather than over it; and there are several species of *Phacops* s.1. (of the *Paciphacops* group discussed below) in which the glabellar lobe 1p is reduced. Late species of *Paciphacops* (*Paciphacops*), such as *P. logani clarkei* Eldredge from the Oriskany of North America, have a reduced lobe 1p, much reduced granulation over the small tubercles of the glabella, 17-18 files of lenses in the eyes, a thickened post-ocular ridge [see *P.* (B.) *delphinoides*], and a tendency toward a linear arrangement of the ornament on the cephalic doublure. For these reasons *Boeckops* is here regarded as a derivative of *P.* (*Paciphacops*). *Boeckops* ranges from the late Pragian to the Eifelian.

4. *Lochkovella* Chlupáč, 1972, with *Phacops miser* Barrande as type, was intended to include a small group of species intermediate in position between *Reedops* and *Denkmannites,* though closer to the former. It is not clear if this intermediate position was judged by Chlupáč to be evolutionary as well as morphologic. In assessing relationship, the narrow pygidial axis and the broad pygidial pleurae, the similarly proportioned thorax, and the very large doublure on the thoracic pleurae are regarded as being of primary importance. Within the main *Phacops* s.s. lineage from *Acernaspis* to *Phacops* s.s., the proportions of the axial and pleural regions remain more or less constant, and the *Reedops* group is essentially the same. However, species of *Denkmannites* and *Struveaspis* are like those of *Lochkovella,* and for this reason they are placed on a separate lineage. It must be noted that members of the Wenlockian-Ludlovian genus *Phacopidella* have similar characters, and the possibility that they also are on this lineage must be investigated. The glabella of *Phacopidella glockeri* is extremely depressed, and in lateral view it tends to be wedge shaped, whereas in *Denkmannites, Struveaspis,* and *Lochkovella* the glabellae are somewhat higher in front, rather like those in members of the main *Phacops* lineage. The glabellar furrows of *Phacopidella* have a distinctive pattern, 3p being strongly connected with the axial furrow, and 1p and 2p being joined by a longitudinal furrow. Its cephalic doublure is also quite short (sag.). *Lochkovella* and its associates are similar to the *Phacops* lineage in these features also. It seems certain, therefore, that the similarities in the pygidium and thorax between the *Denkmannites-Lochkovella* group and *Phacopidella* represent convergence and that the former group arose at a later date from the main *Phacops* lineage.

Chlupáč seems to suggest that *Lochkovella* developed from *Reedops* because of its similar glabella profile. Its anterior border is also greatly reduced, another point in favor of affinity with *Reedops.* However, I still find this view difficult to accept not only because the closely related genus *Denkmannites* was established in late Ludlovian times and *Reedops* is not known to appear until the Gedinnian, but also because the glabellar shape is more similar to some specimens of *Ananaspis* than to species of *Reedops.* In the absence of information on the ventral surfaces, hypostomes, and thoraxes, it is difficult to be sure of relationships.

The main difference between *Denkmannites* and *Lochkovella* is the presence of a continuous anterior border in the former. The other features mentioned by Chlupáč are not of much significance; for example, the eyes of *L. rutherfordi* (Sherwin) are just as reduced as those of *D. volborthi,* and it is difficult to distinguish differences in the impression of the interpleural furrows of the pygidium. For this reason, *Lochkovella* is here regarded as a subgenus of *Denkmannites,* though further work may indicate that the two are synonyms. The relationships suggested in text-figure 4 must be regarded as speculative.

5. It is necessary also to consider the two genera *Bullicephalus* and *Cordapeltis,* established by Přibyl and Vaněk (1970), in relation to both *Lochkovella* and *Denkmannites.* These authors placed both their genera (which are monotypic) in the Phacopidellinae along with *Denkmannites* and *Struveaspis.* The type species of neither genus is well known, the pygidial characters in particular being in dispute. *Phacops bulliceps* Barrande, the type of *Bullicephalus,* is similar in eye structure and in the shape and ornament of the glabella to species of *Eophacops.* In particular, the glabella is constricted at the lateral extremities of furrows 3p, and the eye



Text-figure 4. Relationships proposed for generic groups within Phacopinae.

indents the axial furrow in that position. The furrows 2p and inner 3p are stronger than is normal for *Eophacops,* but these differences are only minor. It is also important to note that *Eophacops trapeziceps* and *Phacops bulliceps* overlap in both geographic and stratigraphic range. Until further evidence is available, it is desirable to assign the species to *Eophacops,* though with some caution (Alberti, 1970, p. 122-123). It is most unlikely that it is a member of the group ancestral to the *Lochkovella-Denkmannites* group.

Cordapeltis koneprusiensis Přibyl and Vaněk, the only known member of the genus, is an Eifelian species; it has a flattened glabella, strong 3p furrows, and large eyes. The surface is apparently granulose. Its affinites cannot be determined on present knowledge.

6. Přibyl and Vaněk also proposed a new subgenus, *Reedops (Signatops),* with type species *Phacops signatus* Hawle and Corda, 1847, and one undescribed species. The morphological details are too poorly known to warrant recognition as a subgenus at this stage.

7. Maksimova (1972) erected a new genus *Paciphacops* with subgenera *P. (Paciphacops),* type species *Phacops logani* Hall, and *P. (Viaphacops),* type species *Phacops pipa* Hall and Clarke. (Eldredge, 1973, concluded that *P. pipa* is a junior synonym of *Phacops cristata* Hall.) I pointed out the importance of the *P. logani* group (Campbell, 1967), but did not formally recognize it as a separate genus. These genera consist of groups of species different from those previously discussed. It is my view that they are sequential groups of species forming part of the main "stem" from *Acernaspis* to *Phacops,* whereas the genera previously discussed are lateral, "dead-end" branches derived from the stem (see text-fig. 3).

There are several features of Maksimova's discussion of the differences between *Paciphacops* and *Ananaspis* and *Phacops* s.s. that appear to be incorrect. Many species of *Phacops* s.s., such as *P. lentigifer* Struve, *P. turco* Richter and Richter, and *P. latifrons* (Bronn), have concave areas beneath the base of the visual surface of the eye. In fact, this seems to be the norm for the genus. There is a lateral border furrow in species of *Phacops* s.s., though in some forms, such as *P. rana milleri* Stewart, it is close to the subocular depression, and the two may even be confluent over part of their length. The lateral parts of the vincular furrow are quite strongly crenulated in most species of *Phacops,* and I know of no species in which it is completely smooth. None of these features can be usd to distinguish *Phacops* from *Paciphacops.* Similarly, *Ananaspis* species have concave areas beneath the visual surface. It would also be difficult to distinguish between the "preoccipital lobe" of *Ananaspis guttulus* and that of *P. (Paciphacops) raymondi.* Consequently, the only remaining distinctive features of *Paciphacops* (according to Maksimova's account) are the genal spines or nodes, and even this may be called in question if *Ananaspic calvescens* Chlupáč has genal spines on some specimens (Chlupáč, 1972, pl. 4, fig. 4).

It is now advantageous to consider the two subgenera of *Paciphacops* separately. *P. (Paciphacops),* which includes not only the *logani* group of North America but also a number of species from the U.S.S.R. mentioned by Maksimova, and *P. crosslei* (Etheridge and Mitchell), *P. latigenalis* (Etheridge and Mitchell), and *P. serratus* (Foerste), from Australia, has advanced beyond the *Ananaspis* stage in (a) the development of a continuous vincular furrow; (b) the presence of perforations in the glabellar tubercles of at least the large-eyed dimorphs; and (c) the presence of a thickened sclera between the lenses in all the small-eyed and most of the large-eyed dimorphs. These characters do not show trends of development; they just appear, and then apparently are transmitted without further development. There are, however, minor advances on some of the trends previously mentioned. Eldredge (1973), for example, has shown that the Siegenian *P. logani clarkei* has reduced granules on and between the glabellar tubercles, and that form, together with the Siegenian *P. logani* subsp. A, shows a reduction in the length of the intercalatory ring almost to the stage exhibited by members of the *cristata* group.

In addition to the above types of characters, some species that are obviously members of the group, for example, the Gedinnian *P. serratus* Foerste and the Siegenian *P. claviger* Haas, produce axial spines on the thoracic segments for the first time in the history of the subfamily. These spines are present in some members of the *cristata* group also, but, as Eldredge has pointed out (1973, p. 329), they are variably developed in related taxa and may not be of much taxonomic value. I accept the view that they are probably sexually dimorphic features.

Members of this subgenus are apparently restricted to the Pridoli-Pragian time interval.

The second subgenus, *P. (Viaphacops),* based on *P. cristata* Hall, has advanced farther along several of the trends toward *Phacops* s.s. These can be summarized as follows:

a. The ornament of the glabella is tuberculate. There are no granules on or between the tubercles, and there are none on the genal regions.

b. The ornament of the cephalic doublure consists of transverse granules that tend to unite to form wavy terrace lines laterally.

c. There is a distinct tendency toward the development of a sigmoidal outline of the cephalic doublure at the lateral ends of the hypostomal suture. The medial part of the suture is straight to concave (see Eldredge, 1973, fig. 20b). This feature cannot be said to be consistent throughout the group; more information is needed.

d. As Eldredge has shown (1973, p. 333), there is a reduction in the number of vertical files of lenses from the *logani* group to the *cristata* group in North America. This has not been quantitatively demonstrated for the Russian material, but an examination of the figures in Maksimova's publications suggests that it is present there also.

In addition, there are characters that appear in the group for the first time but are not spread throughout all members. These are the development of a "ropy" ornament around the lateral and anterior cephalic margins (see Eldredge, 1973, figs. 20c, 31e), and an apparent monomorphism of the eyes. This latter point needs further study.

Finally, there is a reduction of the glabellar lobe 1p and a tendency to incorpoate it medially in the composite glabellar lobe because of the medial reduction of furrow 1p. It was this character that Maksimova used as the chief diagnostic feature of the subgenus. Eldredge ((1973, p. 332), however, found that specimens of *cristata variabilis* from the Emsian to the Eifelian Needmore Formation exhibit a wide range of variation in this character, from almost complete absence to strong development. He concluded that this discovery vitiates Maksimova's concept of *P. (Viaphacops).* This conclusion seems scarcely justified, because both populations of *cristata variabilis* studied showed almost complete reduction of the median part of the lobe 1p in at least some individuals. It cannot be expected that all species groups will show the same rates of progression along the "trends," and it is not unusual to find related species showing quite different ranges of variation in a ggiven character in response to even slightly different selection pressures. Reduction of lobe 1p does seem to be one of the significant features defining the group of species listed by Maksimova.

The depth of the vincular furrow, the narrowness of the occipital ring, and the shortened, weakly segmented pygidium were also listed by Maksimova as characteristic of *P. (Viaphacops).* I see no evidence to support these points. The figures that she gives as representative of *P. (Paciphacops)* and *P. (Viaphacops)* certainly do show quite different pygidia, but they are atypical. In any case, some species of *P. (Paciphacops)* show considerable dimorphic difference in pygidial proportions and segmentation, as is shown below for *P. (Paciphacops) raymondi.* The vincular furrow and the occipital ring in *P. (Viaphacops) cristata* cannot be distinguished from those of *P. (Paciphacops) logani,* on the one hand, and the *Phacops rana,* on the other.

It is important to notice a possible confusion between *P. (Viaphacops)* and *Boeckops,* a genus previously discussed. Both are considered to be derivatives of *Paciphacops,* and they share a number of characters. In particular, both have reduced glabellar lobes 1p. The main distinguishing features of *Boeckops* are the reduced glabellar ornament, the wide occipital ring in relation to the total glabellar width, the low angle of divergence of the axial furrows in front of 1p, the reduced number of axial rings and pygidial pleurae, and the strong taper on the pygidial axis. It is possible to suggest that *Boeckops* was derived from *P. (Viaphacops)* rather than from *P. (Paciphacops),* and this suggestion cannot be ignored. However, *P. (Paciphacops)* is known to have included species with suitably wide occipital rings and reduced lobe 1p (for example, *P. logani* subsp. A of Eldredge, 1973), but no such species of *P. (Viaphacops)* is known. Of course I am not suggesting that there is a direct relation between *P. logani* subsp. A and *Boeckops,* but only that within the *P. (Paciphacops)* group there were suitable morphologies available for the derivation of *Boeckops.*

Full diagnoses of *P. (Paciphacops)* and *P. (Viaphacops)* are given in a subsequent part of this bulletin.

8. Contemporaneous with the early development of *P. (Viaphacops)* are several species that have as much in common with Eifelian species of *Phacops* s.s. as with *P. (Viaphacops).* Examples are *Phacops degener* Barrande and *P. major* Barrande, from the late Emsian of Czechoslovakia; *P. saberensis* Morzadec, from the Emsian of Spain; *P. werneri* Struve, from the late Emsian of the Rhineland; and *P. spedeni* Chatterton, from the late Emsian–early Eifelian of Australia. All these species resemble *Phacops* s.s. in the tendency toward the expansion of the anterolateral corners of the glabella, the marked gradation in size and shape of the tubercles from the back to the front of the glabella, the strong glabellar lobe 1p, and the medially continuous furrow 1p. Unfortunately, the ventral surfaces and hypostomes of most of these species remain unknown, but Barrande's figures of *P. major,* and personal inspection of other material in the Prague Museum, leave no doubt that this species is quite similar to *P. latifrons* in these respects. Morphologies of this type may have developed from advanced species of the *P. (Paciphacops)* type, or from species of the *P. (Viaphacops)* type that had not proceeded too far with the reduction of lobe 1p.

Struve (1972) has proposed several new subgenera within the genus *Phacops.* All of them are from Middle Devonian rocks in Western Europe. They are beyond the scope of this bulletin.

Problem of the origin of the *Eophacops-Phacopidella* group

I have previously suggested that the *Eophacops* morphology was derived from an *Acernaspis* morphology, and this view has been retained herein. A contrary position has been adopted by Destombes (1963, 1972), who believed that the Ordovician *Prephacopidella* (or its senior subjective synonym, *Dreyfussina,* in the opinion of Destombes, 1972, p. 222-223) provided the root stock for *Phacopidella.* Nion and Henry (1966) and Henry and Nion (1970) considered *Prephacopidella* to be a member of the Phacopidellinae, although there are so many uncertainties that the development of a phylogeny is not warranted. Alberti (1970, p. 123, text-fig. 17) indicated an independent origin for *Eophacops* and *Phacopidella* in some unspecified Ordovician stock(s).

Of these authors, only Nion and Henry offer argument in support of their position. From their study of *Prephacopidella hupei* they concluded that the transverse shape of the frontal part of the glabella, the structure of lobe 1p, the form and ornament of the cephalic doublure, the style of the vincular furrow, and the short rounded pygidium all suggest that *Prephacopidella* should be classified with the Phacopidellinae rather than with *Kloucekia.* To these features may be added the remarkably phacopoid thoracic pleural furrows and pleural tips. At first sight, these points, particularly those related to the doublure and the vincular furrow, appear to carry considerable weight. However, there are some further considerations suggesting that they are not conclusive. These are summarized as follows: in no species of *Prephacopidella* are the furrows 3p bipartite; although there is some tendency to isolate lateral lobes on 1p, these are no more distinct than those of, say, *Kloucekia,* but they are much less distinct than those of either *Eophacops* or *Phacopidella;* the furrows 1p do not swing forward at their axial ends, a feature common to all members of the Phacopidae; the thoracic axial rings are not notched; the hypostome has the form of a member of the *Dalmanitina* group; the first, and possibly the second, pygidial rings seem to carry normal dalmanitoid apodemes (see Nion and Henry, 1966, pl. 24, figs. 6-8); the hypostomal suture is strongly concave and is flanked laterally by the rather broad, flattened doublure (see Henry and Nion, 1970, p. 221) in a fashion similar to that of such dalmanitoids as *Calyptaulax* but quite unlike any known phacopoid; vincular furrows are also found in dalmanitoids such as *Kloucekia* (Clarkson and Henry, 1973, p. 113), but they are not necessarily indicative of phacopid relationships; the specimen of *P. hupei* figured by Nion and Henry (1967, pl. 24, figs. 2a, b) shows the muscle insertions on the anterior slope of the glabella, and these have the form of the Pterygometopinae and Chasmopinae rather than of *Acernaspis* (Eldredge, 1971, text-fig. 2h-j); and finally, the species of *Prephacopidella* most reminiscent of *Phacopidella,* viz. *P. hupei,* comes from the Llandeilo, and *Phacopidella* and *Eophacops* are not known until the Wenlock.

It is clear, therefore, that the morphological similarities between *Eophacops* and *Phacopidella,* on the one hand, and *Prephacopidella,* on the other, may be more the result of parallel or convergent evolution than indications of close relationship.

Part of the evidence used to support the *Acernaspis-Eophacops* transition was the similarity between *Acernaspis elliptifrons* (Esmark) and *Eophacops* spp., including *E. musheni* (Salter). The argument, of course, depends on the correctness of these generic assignments. They have not been questioned by subsequent authors, and I see no reason to alter my previous opinion. Recently, through the courtesy of Dr. G. Henningsmoen and Prof. H. B. Whittington, I have been able to examine large and well-preserved collections of both species, and these have yielded some new information. *A. elliptifrons* has a slightly depressed glabellar profile intermediate between *A. orestes* and *Eophacops* spp. The furrows 3p are distinctly bipartite, the posterior part being strongly arcuate and the anterior part well separated from it, but running down almost into the axial furrow. In *Eophacops* the axial furrow is so shallow opposite the palpebral lobe that the anterior part of furrow 3p runs into it. The 2p furrows and the pattern of muscle scars on the anterior part of the glabella of *A. elliptifrons* are similar to those of both *A. orestes* and *E. musheni* (see pl. 1, figs. 1, 2). The pygidial muscle scars consist of the usual two sets of the phacopinae, one formed of transverse, convex-forward scars on the flanks of the axial rings, the other of more equidimensional scars along the axial furrow. Similar sets are described below in *Paciphacops* and *Reedops. E. musheni* has a similar pattern, the only difference being that the scars in the axial furrow are more elongate and become confluent posteriorly. The shape of the hypostomal suture and the anterior and lateral parts of the cephalic doublure in both *A. elliptifrons* and *E. musheni* have almost exactly the same pattern as *A. orestes* and the later Phacopinae. Finally, the thoracic axial rings of both *A. elliptifrons* and *E. musheni* have the distal nodes of the Phacopinae.

These data indicate that *Acernaspis* and *Eophacops* are distinguishable only in minor features, and for almost all characters it is possible to produce a graded series of morphologies between them. This can be interpreted to mean (a) that one morphological type evolved from the other, (b) that both evolved from some earlier unknown morphology that had already developed the features mentioned above, or (c) that the similarities indicated are the result of parallel evolution. The last view is unacceptable to me because, unlike the comparison between the cephalic doublure and vincular furrow of *Prephacopidella* and *Eophacops,* these similarities involve virtual identity of structure. The second interpretation above may be true, and it avoids certain problems such as the peculiarity of the depth and form of the axial furrow opposite the anterior ends of the palpebral lobes of *Eophacops,* which show considerable similarity to the furrows in several Ordovician genera. However, there is no record of an *Eophacops*-like line in the Early Silurian, and hence I prefer to reject this hypothesis.

The features *Phacopidella* has in common with *Eophacops* were listed by me (Campbell, 1967). The genus is typically phacopid in the structure of the lateral and intercalating parts of lobe 1p, the bipartite structure of lobe 3p, the lack of genal spines, the notching of the ends of the thoracic rings, the form of the thoracic pleural furrows, and the lack of true apodemes on the pygidium. The main difficulty with the hypothesis that the genus originated in *Eophacops* is the relatively large number of segments in the pygidium, or, put in another way, the relatively large size of the pygidium with respect to the cephalon. This should be seen as a correlative of the increased relative width and depression of the whole skeleton. With shorter downturned pleural tips for a given angular rotation, the thorax would be able to cover less of the ventral surface of the cephalon during enrollment, and hence the pygidium would have to be increased in relative size. Presumably, therefore, *Phacopidella* may be regarded as an adaptation of the *Eophacops* morphology to a mode of life requiring a wide, flat exoskeleton. No morphological discontinuity is present in such an adaptation. It should also be noted that some such explanation would be required if

Prephacopidella were accepted as the source of *Phacopidella.*

Dimorphism in phacopids

Suggestions that populations referred to species of "*Phacops*" exhibit sexual dimorphism have a long history going back at least to Barrande (1852). Recent reviews and comments on the subject are to be found in work by Clarkson (1966), Selwood and Burton (1969), and Eldredge (1973), the last-mentioned author having added many new data.

In the light of the above criteria I accept the conclusions of Eldredge that *P. logani raymondi, P. l. logani,* and *P. l. birdsongensis* are sexually dimorphic or trimorphic, though in the case of *logani logani* the evidence is not unequivocal (see below). Eldredge's work, following similar lines to that of previous investigators (Girty, 1899; Tansey, 1922), concentrates on the number of lenses and the number of files of lenses in the eyes. There is no doubt that this is often the easiest (though not the only) way to recognize the presence of dimorphism in this group, but many species are not dimorphic in the eyes at all (see Eldredge's 1972 discussion of *P. iowensis,* for example). In addition to eye morphology, Selwood and Burton (1969) recorded dimorphism in the following characters:

1. Glabellar granulation (tuberculation).
2. Glabellar lobe 1p proportions.
3. Proportions of the occipital ring.
4. Ornamentation of the genal region.

All these modes can be found in some members of the *P. logani* group, which also exhibits many additional modes. These are:

5. Relative size of the sclera between the lenses.
6. A median tubercle on the occipital ring.
7. Large perforations in the glabellar tubercles.
8. Depth of the posterior border furrow.
9. Depth and outline of the palpebral furrow.
10. Depth and divergence of the cephalic axial furrows.
11. Inflation of the palpebral lobe.
12. Presence or absence of a rim to the palpebral lobe.
13. Depth of the vincular furrow.
14. Inflation of the lateral nodes on the thoracic rings.
15. Number of pygidial axial rings.
16. Number of pygidial pleural furrows.

The hypostomes may show some dimorphism, but insufficient specimens are available to be sure of this.

It seems that almost every part of the animal may be involved, though the differences may be slight and are likely to be overlooked, especially if the preservation is poor. If the differences are observed and only a few specimens are known, the dimorphism is usually ascribed to variation in a monomorph. Despite the length of this list, it is certainly not exhaustive. Various authors have considered the possibility that the large axial spines on some species may be dimorphic (Etheridge and Mitchell, 1895; Sherwin, 1971a; Eldredge, 1973) but have favored the view that they are not. However, the case of *crosslei* Etheridge and Mitchell and *serratus* Foerste, recently examined by Sherwin, involves two groups found at the same localities and horizon, differing in the following main characters:

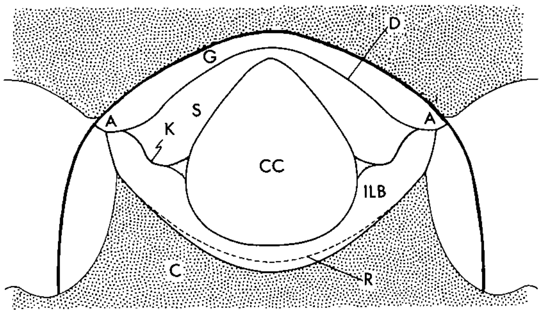
1. Number of lenses and files in the eyes.
2. Depth and divergence of the axial furrows.
3. Size and shape of the posterior border furrow.
4. Presence or absence of an axial spine on the occipital ring.
5. Presence or absence of axial spines on the thorax.
6. Number of pygidial axial rings.

That is, they show the normal modes of dimorphism plus that of the thoracic axial spines.

Eldredge records that *P. cristata variablis* shows axial-spine development as "variable both within and among population samples" (1973, p. 329). In the light of the above discussion this evidence also supports the view that axial spines are dimorphic.

Phacops logani birdsongensis Delo, which is shown below to be trimorphic, is of particular interest. There is a large-eyed morph with 17 files of lenses, a small-eyed morph with 14 files (1 specimen with 15), and an intermediate morph with 15 files. The intermediate is similar to the small-eyed morph in eye characters, but it matches the large-eyed morph in all other characters except the shape of the palpebral furrow.

Selwood and Burton (1969) reported the existence of three eye morphs in *P. schlotheimi schlotheimi* and noted that "Except for the occipital ring ornament which is light in Forms A and B but heavy in Form C the polymorphs are otherwise identical". This is apparently similar to the situation observed in *P. birdsongensis*.



Text-figure 5. Semidiagrammatic medial section of lens from eye of large-eyed specimen of *P. (Paciphacops) birdsongensis* (Delo) partially preserved in silica. Reconstructed from several specimens from Pickwick Dam, as mentioned in text.

Lens structure in the Phacopina

Clarkson (1966, 1967, 1969, 1974) summarized previous knowledge of this topic and added much new information. Several problems have proved intractable, mainly because of the quality of the lens preservation. The material of this study has provided some well-preserved carbonate specimens and others in which partial replacement by silica has yielded new information.

Paciphacops birdsongensis

Silicified specimens.—In the large-eyed morph from the Ross Limestone, Pickwick Dam (USNM 20891 A-C, 20892 A-D), the lenses have been partially replaced and partially infilled by silica, whereas the exoskeleton and the interlensar sclera have been completely dissolved. The silicification is highly irregular both within and between specimens, so that the interpretation of any lens is always difficult and often is ambiguous. The interpretation offered here is the result of piecing together information from several individuals.

The columns occupying the sublensar alveoli are usually formed of silica, but they sometimes also contain fine detritus. The corneal membrane either is not replaced or is removed with the external mold. Consequently, the eyes are usually preserved as columns of silica (C) on the top of which is the irregular siliceous replacement of the subcorneal parts of the lenses. Viewed from the outside, the most complete lenses (pl. 6, figs. 6-11) show a narrow, slightly concave annulus (A) around a flat dome (D), the center of which is broken away to form a pit with a median boss (B). This is interpreted to mean that the surface (D) was originally complete and that the boss lay immediately beneath it. In lateral view the columns expand toward the external surface, forming a flange. The annulus mentioned above is formed by the outer surface of this flange. The lens replacement forming the dome (D) is sometimes of solid silica, or sometimes it is only a siliceous film that is easily broken away. In either case, this surface seems to represent the junction between two lens units. There is always a gap (G) between this surface and the external surface, which presumably represents the corneal membrane and comes away on the external mold. The dimensions of the gap (G) are difficult to estimate. Presumably it was occupied by the "upper unit" of Clarkson.

When the dome (D) is broken away, a central core (CC) is exposed. In some lenses this core is solid, in others hollow, and in yet others the outline of the body seems to be formed by a cavity within which there is a solid center. Consequently, it is difficult to be sure of the shape of the central core. Its proportions are approximately as shown, but its crest may be either sharper or blunter, and its total form may be more pear shaped. Its base lies close to the lower surface of the lens, but the two are not contiguous. At some sites, the lens comes freely away from the column (C), leaving a completely smooth surface that must represent the mold of the basal lens surface. At other sites, there is a rough layer (R) coating this surface. It may represent a thin basal layer. Occasionally there is a rough, irregular surface (K) surrounding the central core. This must represent the contact between the lower component of the upper unit and the intralensar bowl shown so well in *raymondi,* but its shape is quite different in the two species. The nature of the junction between the surface (K) and the central core cannot be determined.

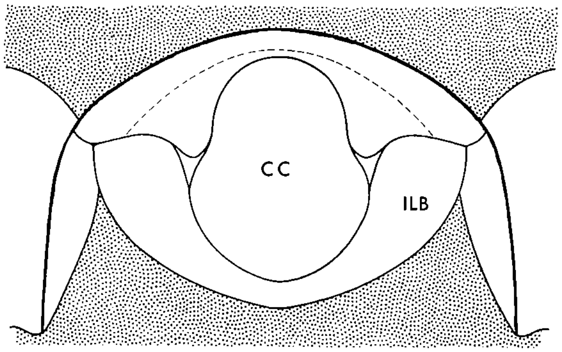
The mold of the base of the sclera has weak median ridges between the lenses, and these form slight peaks at the triple junctions. Thus, there are weak median furrows on the sclera, and these form pits at the junction between adjacent lenses.

Large-eyed calcareous specimens. —Several specimens have been polished (ANU 30593, USNM 208985A). Most of them have the lower parts of the lenses replaced with matrix, and those that remain calcareous have been extensively recrystallized. Other specimens have been studied by immersing the lenses in oil and examining them from the exterior.

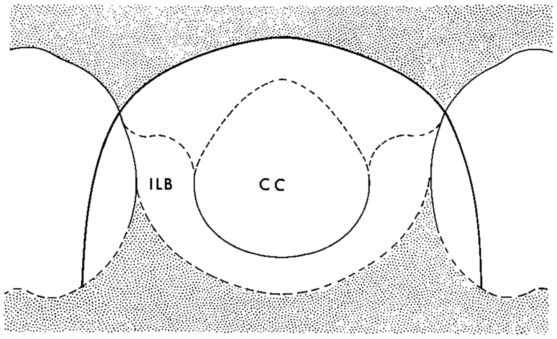
The bases of the lenses are never well preserved, and the presence of a basal layer cannot be established. The intralensar bowls are clearly defined against the central cores in several specimens, but the boundaries with the upper unit are vague. The upper part of the central core cannot be distinguished on any section, but slightly weathered specimens often show it quite clearly. Apparently it is composed of more homogeneous calcite than the surrounding tissue and tends to weather out as a dark mass in lighter colored material. It is usually broadly rounded on top. No differentiation in the tissue between the central core and the cornea is apparent.

There are obvious differences between this interpretation of *birdsongensis* and the one based on the silicified specimens, particularly in the shapes of the central core and surface (K). These differences may be real, and they may indicate that the two collections, which come from different stratigraphic units, are not really conspecific, despite the fact that they cannot be distinguished by any other characters. On the other hand, it is possible that the silicified material has been misinterpreted; this applies particularly to the shape of the surface (K), which is always poorly preserved.

Small-eyed calcareous specimens.—Too few specimens are available for more than one to be sectioned (USNM 208985B). This individual shows the central core, the intralensar bowl, and the upper unit, both in section and on weathered external surfaces. As far as can be determined, there is little difference between these eyes and those of the large-eyed morph, even in the proportions of various elements.



Text-figure 6. Semidiagrammatic medial section of lens from calcareous large-eyed specimen of *P. (Paciphacops) birdsongensis* (Delo) from Birdsong Shale, based mainly on USNM 2089985A, and ANU 36890. For explanation of symbols, see text.



Text-figure 7. Semidiagrammatic medial section of lens from calcareous small-eyed specimen of *P. (Paciphacops) birdsongensis* (Delo) from Birdsong Shale, based on USNM 208985B. For explanation of symbols, see text.

Paciphacops raymondi

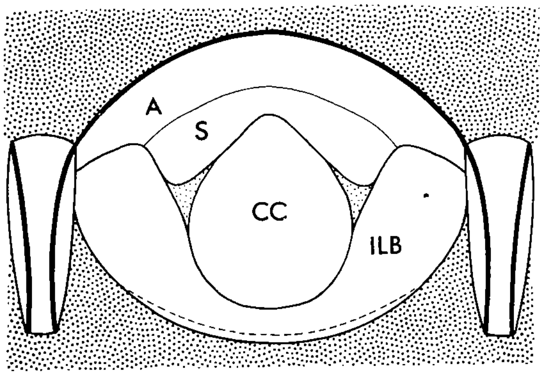
Large-eyed morph.—These lenses are often badly corroded and can usually be studied only on polished surfaces. They do not all yield comparable results, presumably because of recrystallization and (or) chemical replacement.

The best preserved individual (OU 7219C) was polished down a file. It has the lower unit of each lens removed and replaced by matrix. The remainder of the lenses are composed of four clearly distinguishable units. These are whitish in color and are separated by films of clear calcite, and although they are not all visible in all lenses, there is no doubt of their existence. The cornea is thin and cuts to the bottom of the sclera. Inside that is an upper unit that has the usual mushroom shape. Its lateral contacts with the intralensar bowl are quite sharply defined. Two components (A and S) may be distinguished within the upper unit, the contact between them being rather vague. There is a slight difference in color, and laterally there is a clear boundary, but this fades axially. Beneath the component (S) at some sites there is a clearly defined globular body that seems to be the homologue of the central core (CC) of other species described herein. The base of this central core is not always present.

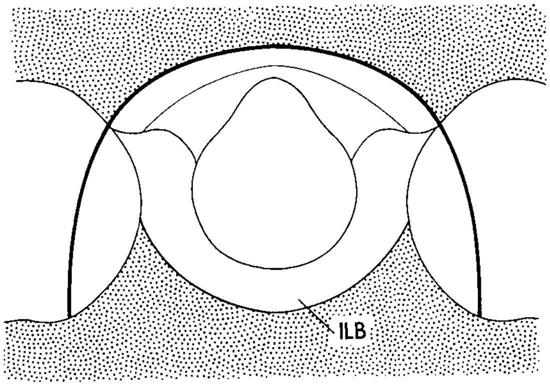
In some specimens the intralensar bowl is partly or completely preserved in clear calcite, but in others it is replaced by matrix (OU 7218A-B). Often the base of the central core is clearly preserved, and the lower component of the upper unit can be vaguely distinguished. None of the specimens shows a clear differentiation between basal layer and intralensar bowl, but this is probably the result of poor preservation. Finally, in some individuals in which ferruginous replacement has taken place (OU 7218) the central part of the upper unit seems to be preferentially replaced. It is not clear to me that this is replacement of a primary structure, but it occurs sufficiently commonly and in a sufficiently regular way to suggest that it is.

Small-eyed morph.—The lenses in OU 6619A-C, OU 6620, and USNM 208984A are not nearly as well preserved as those of the large-eyed morph, but enough is visible from sections and transparent lenses viewed from the exterior to permit comparison to be made.

The outer lens surface has less than half the convexity of the inner surface and is covered by a very thick cornea. The intralensar bowl is commonly replaced by matrix, but at some sites it is defined by a clear basal layer. In comparison with the other morph it extends farther up the sides of the lenses. The sclera breaks the outline of the intralensar bowl laterally, forming a somewhat irregular lens shape. The base of the central core is often clearly defined, but in sections it has not been possible to distinguish its upper limits, nor has any differentiation of the upper unit into two components been observed in sections. However, several slightly worn specimens that have the lenses partly replaced have added further information. This replacement is similar to that described for the other morph. Although the shape of the upper part of the central core cannot be precisely determined, it is large and extends at least up to the level of the surrounding sclera. The upper unit is clearly differentiated into two components, the outer one being very thin.



Text-figure 8. Semidiagrammatic medial section of lens from calcareous large-eyed *P. (Paciphacops) raymondi* (Delo) from Haragan Formation, based mainly on OU 7219C. For explanation of symbols, see text.

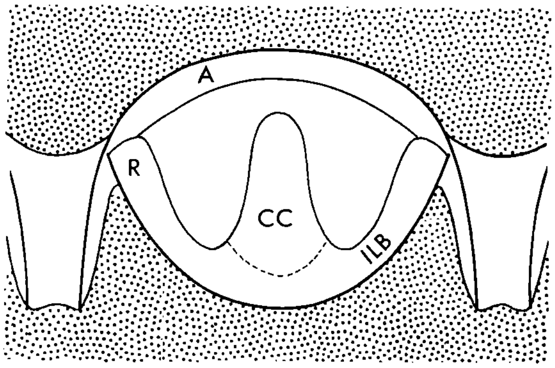


Text-figure 9. Semidiagrammatic medial section of lens from small-eyed *P. (Paciphacops) raymondi* (Delo) from Haragan Formation, based largely on OU 6619C. For explanation of symbols, see text.

Reedops deckeri

Three eyes have been sectioned (OU 6557, OU 6618, and USNM 208983A), and several other specimens have eyes that are either sufficiently worn or have lenses sufficiently transparent (OU 5376-7) to permit an examination of lens structure. The internal structure of the lenses is distinguishable by (a) variations in the color of the calcite components, (b) a thin layer of ferruginous material along the boundary surfaces of the components of some and inside others, (c) the presence of irregularly distributed dark-colored minerals along these surfaces.

The lenses are unequally biconvex, the outer surface having about half the convexity of the inner. The height/width ratio of the lenses varies from 3/4 to 3/5. In section, a lower component that is apparently the homologue of the intralensar bowl, or possibly the intralensar bowl plus the basal layer, is clearly visible. No clear differentiation of these two structures has been observed. The intralensar bowl is thickened around its upper rim to form a solid ring (R). Occasionally there are slight irregularities on the inner wall of this ring, and these may be compared with the diaphragms of Clarkson. They are not observable within the ring itself, however, and they are probably only irregularities in the preservation. A distinctive feature of the intralensar bowl is the presence of a central core. In section this cannot be differentiated around its base from the remainder of the bowl, and although its upper limits are indefinite at some sites, at others they are clearly outlined by a ferruginous layer.



Text-figure 10. Semidiagrammatic medial section of lens from *Reedops deckeri* Delo from Haragan Formation, based largely on OU 6557 and USNM 208983A. For explanation of symbols, see text.

There is an upper unit that can be differentiated from the intralensar bowl by color or compositional changes, and, as with other phacopids, the upper unit has a clearly defined lip around its outer margin, where it overlaps the intralensar bowl. In section the upper unit appears to be homogeneous, but viewed from the outside its bipartite nature can be clearly seen. Beneath the corneal membrane there is a relatively thin layer (A) that is completely ferruginized at some sites but at others is preserved in clear calcite, although in the latter case the corneal membrane is sometimes preserved as a ferruginous coating. The central core (CC) is usually visible and is preserved either as clear calcite or as ferruginized substance, or as matrix, the different forms of preservation being found even within the one eye. The tip of the core reaches up almost to the layer (A), which is higher than is seen in the sections. There is some variation in relative proportions of the various layers both within and between eyes.

The thick corneal membrane penetrates the sclera, the bottom edge of which lies a little below the alignment of the bases of the lenses.

The most obvious feature of this kind of eye is its similarity to species of *Paciphacops*, even though the base of the central core cannot be distinguished. This feature may have been rather vague in the original lens, and its preservation may depend on some chance phenomenon. At first sight there seems to be little similarity between *R. deckeri* and the species of *Reedops* figured by Clarkson, but it must be remembered that the interpretation of *deckeri* offered here is a composite, based on several differently preserved lenses.

Interpretation.—1. All the North American phacopid species examined, viz., *P. raymondi, P. birdsongensis, P. rana,* and *R. deckeri,* have essentially similar lens structures: a corneal membrane, an upper unit divisible into external and internal members, a central core, and an intralensar bowl which may or may not have a basal layer. The central core is at least partly homologous with the proximal nucleus of Clarkson, but that term has been used to refer to an apparently specialized condition in *Ananaspis* (Clarkson, 1969, text-fig. 6j). The so-called ghost structures in the intralensar lumen of *R. sternbergi* may be part of the central core. The use of a new name seems justified.

2. There are considerable differences in the structures visible in the lenses of one species from one locality and in some cases even in the lenses of one eye. Also, structures seen in tangential section are often not visible in vertical sections of any orientation. This has been seen to be the case in all species examined, but it is especially well shown in the figures of *P. rana* given by Towe (1973). In his figure (b), the successive rings represent the corneal membrane, the annulus, the external and the internal members of the upper unit, and the central core. (Some of them may be ground down so that the matrix replacing the intralensar bowl is exposed.) In the vertical sections of figures (c) and (d), no such layers can be differentiated. The internal structure of lenses cannot be determined from vertical sections only.

This point is of importance in determining the lens structure of species of *Reedops*. According to Clarkson, the upper units in *R. cephalotes* and *R. sternbergi* are homogeneous. However, specimens of these species from the classic Barrandian localities are usually sufficiently recrystallized to destroy any differentiation in this unit.

3. The two morphs of a single species may show differences in internal structure of the lenses, as well as in gross eye morphology. The internal differences may not be radical, but there are certainly differences in the proportions of the main components in some species.

4. The thickened ring similar to that figured by Lindström (1901) at the top of the intralensar bowl in *P. macropthalamus* is common to most phacopids. It is an artifact produced by viewing a thickness of clear calcite. It is also possible that diaphragm-like structures in this position are produced by vagaries of preservation within this part of the bowl.

5. The intralensar bowl seems to be less stable chemically than the remainder of the lens. It is completely replaced by matrix in many specimens of all species examined, the matrix making a sharp contact with the central core and the upper unit. Presumably, solution of the bowl took place at an early diagenetic stage. It must have been of slightly different composition from the remainder of the lens.

6. The basal layer is extremely difficult to distinguish in most of the specimens examined, and it is never as thick as those described by Clarkson in various European species.

7. As has been pointed out by Clarkson (1969, p. 202), it is difficult to see how "nucleate" lenses of the type figured for *Ananaspis* could give rise to the "non-nucleate" lenses of *Reedops,* but part of the problem may be in the interpretation of *Ananaspis*. If the figures of *A. communis* (Clarkson, 1967, text-fig. 1c; 1969, text-fig. 6j) are compared with those of the large-eyed morph of *P. raymondi* given herein, the proximal nucleus and the central core are seen to be comparable in position and shape, and the intralensar bowls are also similar. If, in the specimens of *A. communis,* the lower member of the upper unit (S) were preserved in the same medium as the intralensar bowl, the two species would have almost identical morphologies. This is not surprising, as *Paciphacops* is thought to have been derived directly from *Ananaspis*. Given this interpretation, and the comments above on the structure of the upper unit in *R. sternbergi* and *R. cephalotes,* it is not difficult to derive the *Reedops* lens structure from that of *Ananaspis*.

Exoskeletal perforations in the Phacopina

In thin and polished sections, all parts of the exoskeleton of *Paciphacops* (*Paciphacops*) are seen to be perforated. The openings of the perforations have been observed on the external surfaces of both *raymondi* and *birdsongensis* (see pl. 6, figs. 1, 2). Perforations observed fall into two categories: (a) those of large diameter, which are usually situated in the axis of tubercles on the glabella, the palpebral area, and the axial rings of the thorax and pygidium; and (b) those of small diameter, which are densely packed and are distributed over the whole surface of the exoskeleton. Both types penetrate the entire thickness of the preserved exoskeleton.

1. The large diameter perforations are not

invariably axially placed in the tubercles. Those on the front of the glabella, for example, often run obliquely upward through the tubercles and open on their upper (dorsal) faces. Further, not all the tubercles on any one specimen are seen to be perforated. The perforations vary considerably in diameter; on large-eyed *birdsongensis* and *raymondi* they are 25-35μ in diameter throughout most of the exoskeleton, though they expand to as much as 75μ at the external surface. Around their openings on the inner surface there is a slightly raised collar similar to that reported by Evitt and Whittington (1953, pl. 9, fig. 14) in *Flexicalymene* and by Dalingwater (1973, pl. 108, fig. 3) in *Illaenus*. These also occur in dalmanitids (see below). Perforations of this size do not occur in the small-eyed morphs of either *birdsongensis* or *raymondi*. The tubercles in these morphs carry only fine perforations like those in the remainder of the exoskeleton.

The size and distribution of these large perforations suggest, by analogy with living arthropods, that they carried tactile sensory setae. The presence of the raised collars around their internal openings, like those of many other trilobite groups, is of interest. Presumably there was a thin uncalcified layer over the inner surface, but this could scarcely have modified the shape of these collars. Examination of living decapods shows depressions, rather than collars, around the setal openings to accommodate the enlarged cells at the base of the setae. The function of the collars remains unknown.

2. The fine perforations are up to 10μ in diameter and are spaced at 20-50μ on the external surface, much closer than the surface granules, to which they bear no relation. They are smooth-walled tubes showing no evidence of spiral structure and set approximately at right angles to the exoskeletal surface. They open on the surface of the glabellar furrows, the vincular furrow, the articulating half-rings, and at least the anterior part of the cephalic doublure. On all parts of the skeleton, they open on and between the elements of the ornament. They are present in both large- and small-eyed morphs.

The presence of the fine perforations in skeletal tissue overlying regions of muscle attachment (the glabellar furrows), and in the articulating half-rings, indicates that they were not occupied by tactile sensory structures. Rather, their existence on all parts of the exoskeleton and their relatively uniform spacing suggest that they had some function in relation to the deposition of some or all of the exoskeleton, to ecdysis, or to the passage of substances through the skeletal tissue. Living arthropods have only two types of perforations that are comparable: the pore canals and the tegumentary ducts. The comparison is closer with the tegumentary ducts in most features—diameter, nonspiral shape, and spacing—though they are possibly more regularly distributed than is normal in modern forms. The possibility that some of the perforations in various trilobite groups may be tegumentary ducts has been commented on by Rolfe (1962, p. 43) and by Dalingwater (1973, p. 837). These structures in various living arthropods have been studied in detail, the most comprehensive account being that of Yonge (1932), who reported their presence in a large variety of both primitive and advanced crustaceans; they are known to occur in other arthropods as well. According to Yonge (p. 310), they are "distributed everywhere beneath the surface of the integument, in the foregut and hindgut and in the gill chamber as well as over the entire surface of the body, in all Decapod Crustacea." He concluded that the tegumentary glands were responsible for the deposition of the epicuticle (misnamed the cuticle) over the surface of the chitinous layer of the exoskeleton. This interpretation has been accepted as *one* of the functions of these glands by later workers (see Richards, 1951, p. 214-215, and Dennell, 1960, p. 461-463, for summaries), though they may have several additional ones.

Thus, the available evidence suggests that at least some trilobites had tegumentary glands, and hence a true epicuticle. No distinctive layer, however, that could be recognized as such is found on the specimens of *birdsongensis* or *raymondi* that I examined. Presumably it would have been a hardened organic layer and consequently lost during preservation. The calcified layer that is termed epicuticle in many trilobites is probably incorrectly identified.

These interpretations leave no explanation for the granules on the skeletal surface, a feature of the *Ananaspis-Paciphacops* group. There is no evidence that they are coincident with any perforations nor that they have depressions in their crests that might have housed the basis of sensory structures. Their significance remains a mystery.

Paciphacops (Paciphacops) Maksimova 1972

Type species.—Phacops logani Hall from the Helderberg of New York.

Diagnosis.—Moderate size for subfamily. Glabella is moderately inflated but rarely overhangs the anterior border; axial furrows diverge at 60°-75° in front of lobe 1p; lateral lobes of 1p are high and equidimensional, and intercalating ring is well defined; glabellar ornament consists of tubercles of one or two orders intermingled; granules are superimposed on tubercles over the entire glabella or only on its anterior face; tubercles are of similar size on all parts of glabella; ornament on remainder of cephalon is granulate; eyes are dimorphic or rarely trimorphic; there is a thick sclera in all small-eyed and most large-eyed morphs; doublure is covered with granules; hypostomal suture is straight or slightly convex; hypostome itself is strongly convex, with a very short posterior border and three short posterior marginal spines; hypostomal ornament is granulose; maculae are set well forward; pygidium has 6-9 axial rings plus a terminus; interpleural furrows are well defined; pygidial axial ornament consists of weak tubercles plus granules, or granules only; pleurae are granulate; dimorphism is apparent in numerous features, such as coarse perforation of the cephalic tubercles, dimensions and divergence of cephalic axial furrows, occipital and thoracic tubercles, and pygidial proportions.

Remarks.—This subgenus has been commented on and its relations discussed in the remarks on the subfamily.

Paciphacops (Paciphacops) raymondi (Delo, 1935)

Pl. 6, figs. 1, 3; pl. 7, figs. 1-3; pl. 8, figs. 1-4; pl. 9, figs. 1-3; pl. 10, figs. 1-3; pl. 13, figs. 1, 2

Phacops hudsonicus Hall; GIRTY, 1899, p. 571, pl. 61, figs. 4a-d.
Phacops raymondi DELO, 1935, p. 423, pl. 48, figs. 2, 3.
Phacops raymondi DELO, 1940, p. 24, pl. 1, figs. 20, 21.
Phacops logani raymondi Delo; ELDREDGE, 1973, p. 297-298, figs. 3a-h.

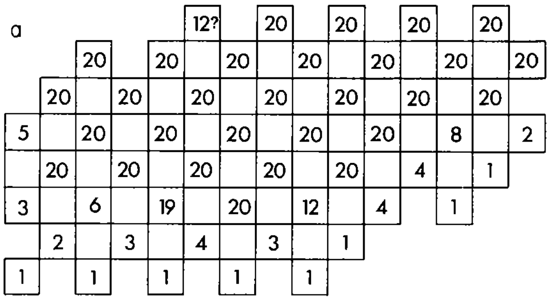
Diagnosis.—Of average size for the genus; strongly dimorphic. Large-eyed morph has slightly protrusive glabella; shallow axial furrows; faint occipital node; perforate glabellar tubercles are covered with granules toward the front but not the back of the glabella; eyes have 80-116 (average 98) lenses in 16-19 (mode 16) files; pygidium is slightly elongate, with 9-10 rings plus terminus, and 8-9 pleural furrows. Small-eyed morph has rounded, protrusive glabella; strong axial furrows; prominent occipital node; imperforate glabellar tubercles are covered with granules; eyes have 30-48 (average 35) lenses arranged in 12-15 (mode 14) files; pygidium is squat, with 7-8 axial rings plus terminus, and 6-8 (usually 7) pleural furrows.

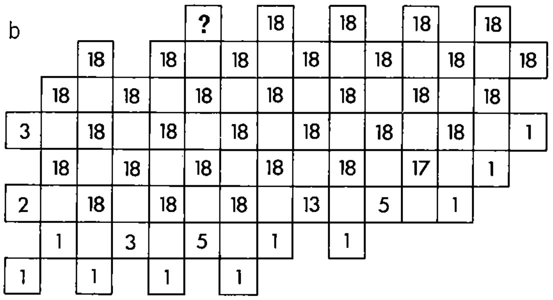
Small-eyed form

Description.—Largest specimen has glabella 18 mm long, but the average length for the collection is only 10 mm; maximum/minimum glabellar width averages 19/10; maximum glabellar width/width of cephalon averages 10/17; glabellar length/glabellar width averages 0.93 (range 0.90-1.00); forward of furrows 1p, axial furrows diverge at 60°-80°; axial furrow is deep, with an almost vertical wall against the glabella but a more inclined wall against the cheek; in anterior profile, lateral walls of glabella are vertical or occasionally even slightly convergent downward; top of glabella is highly arched; in lateral profile (in standard orientation), glabella rises gradually to a high crest well in front of the eyes, then drops vertically to the anterior border, which it slightly overhangs; occipital ring is high, with its highest point toward the rear, dropping abruptly in front into the deep, short (sag.) occipital furrow; squat, broadly based occipital node is present on most specimens, producing a markedly triangular posterior profile for the whole ring; occasional specimens have the node barely visible; lateral occipital nodes are transverse, not inflated, and in posterior profile break the contour of the ring only slightly, if at all; nodes are semi-isolated by a strong incision in the front of the ring and a very vague, more lateral indentation on the back of the ring. Lobe 1p has sharply defined lateral nodes, is subcircular in outline, subconical in form, and is depressed well below the level of the adjacent glabella; intercalating ring is variably developed, at one extreme forming a faint, depressed, unornamented rise between furrows 1p and 2p, and at the other a clear ring, continuous in profile with the anterior part of the glabella and carrying many tubercles of the usual glabellar type. Furrow 1p is deep and with a vertical front wall at the apodemes but normally fades away abruptly toward the midline, where it is interrupted by normal ornament; some specimens (those with lobe 1p poorly developed, see above) have a continuous depression in the position of furrow 1p (see pl. 8, fig. 1b); furrow 2p is curved, not meeting the axial furrow; medial part of furrow 3p is much more highly curved; lateral part of furrow is completely isolated and meets the axial furrow opposite the extreme anterior edge of the eye.

Posterior border is highly and evenly arched and bears a pronounced articulatory flange between the axial furrow and the fulcrum; lateral to this it lengthens (exsag.) abruptly and flattens to the genae. Posterior border furrow is only faintly flexed and has steep equally inclined walls front and back and a U-shaped cross section; at lateral extremity, posterior furrow makes a subangular junction with the lateral border furrow that fades slightly as it crosses the sutural ridge and then broadens to form a shallow, open structure swinging below the eye to the axial furrow. Genal angles are subangular, and some have genal nodes.

Palpebral furrow is parallel to the axis posteriorly, curving inward anteriorly, where it cuts down deeply into the axial furrow; furrow is shallowest opposite midlength of eye, then deepens abruptly to the rear, where it swings around the end of the eye into the deep sutural furrow that widens abruptly into the lateral border furrow. Palpebral area lies well below the level of the glabella. Palpebral lobe is a little lower than the palpebral area, turns down markedly laterally, and is bordered by a pronounced rim that is set even lower than the main part of the lobe; in lateral profile this rim is not horizontal but is lowest above file 7. Eyes consist of 30-48 (average 35) lenses arranged in 12-15 (mode 14) files; typical arrangement 232 323 333 232 21; statistical pattern as shown in text-figure 11; distance between centers of adjacent lenses in a file averages 0.50 mm in adult specimens; largest lenses are approximately 0.40 mm in diameter;





Text-figure 11. *a*, statistical pattern of lenses in 20 specimens of small-eyed *P. (Paciphacops) raymondi* (Delo) from Haragan Formation at Old Hunton Townsite.

b, same for 18 specimens of same species from Haragan Formation at White Mound.

These diagrams record the number of specimens carrying a lens at each position, the vertical columns representing the lens files. The anterior of the eye is invariably at the left of the diagram. Counting begins with the most dorsally placed lens in the anterior file and then proceeds to successively more posterior files. A basic pattern for the most dorsal lenses in the first few files rapidly becomes apparent, and variations of the pattern by the insertion of an "abnormal" first file can then be recognized. The main variation is produced by the addition of lenses at the ventral ends of the files. Variation in the number of files is usually due to additions at the posterior end, but occasionally a morph shows addition at the anterior end, as does the one in this figure. Occasional variations occur by the omission of a lens at the dorsal end of a file. Where small lenses occur in the latter positions they have been counted as though they were normal. In the morph of text-figure 11 the dorsal lenses are usually small, and with poor preservation it is invariably difficult to determine if a lens is present at this end of file 6. In the Old Hunton Townsite specimens, it could be distinguished in 12 specimens but may have been present in more. The number present in the White Mound collection could not be reliably estimated.

sclera between lenses is inflated, granulose, and forms a hexagonal framework, in which the lenses sit in crater-like depressions; lenses have sufficient convexity to protrude beyond general level of scleral surface; internal structure of lenses and sclera as discussed above; base of eye is formed by a broadly swollen band normally placed well below the lowest lens, the space between it and the lenses being filled with sclera; below this, the cheek is normally concave and drops steeply into the border furrow, but in several specimens this concavity is separated from the border furrow by a swollen band of varying height (see pl. 10, fig. 3b). Post-ocular part of fixed cheek abruptly drops in height from the palpebral area and has a "pinched-out" appearance between the sutural and posterior border furrows; $\frac{H}{A}$[1] varies from 0.18 to 0.30 (average 0.22), and $\frac{A}{G}'$ varies from 0.44 to 0.49 (average 0.46). Posterior limb of facial suture lies in a pronounced postocular furrow.

Doublure has an almost straight hypostomal suture medially, curving back gently at its lateral extremities; vincular furrow is strong around the whole cephalon and on each side carries 9-10 strong notches; inner wall of notched part of furrow is at least as strong as the outer wall; median length of doublure (measured from posterior edge of vincular furrow) is about 0.33 times total glabellar length.

Ornament of glabella consists of moderately large tubercles (0.2-0.5 mm in diameter) over most of the surface, with smaller tubercles between them, particularly on the front of the composite lobe; tubercles on occipital ring are more subdued than those on glabella; tubercles on inner parts of fixed cheeks are like those on glabella, but those on the postocular ridge are much weaker; on palpebral lobe, tubercles are comparable to those on the occipital ring; all above-mentioned tubercles (except small ones on front of glabella) are covered with granules; borders and palpebral rim have granules only; concave surface of free cheek below eye has finer and sparser granulation. Doublure also is granulose, with granules more or less equidimensional and discrete.

Hypostome width (excluding anterior wings) is approximately equal to length; central body is highly swollen in both lateral and posterior profiles; in ventral view, lateral margins are almost straight and converge slightly back to the posterior wings, then converge more strongly to the posterolateral corners, where there are tiny spines; posterior margin has a slightly larger median spine forming the posterior extremity; in lateral profile, prominent posterior wings are situated a little in front of the mid-length and produce a deep antennal notch; behind the posterior wings, the margin sweeps gently upward; middle furrow is broad and barely distinguishable, extending from near the anterolateral corners and producing a slight downturn of the central body along the hypostomal suture; maculae are large and are situated just forward of a line joining the posterior wings; border furrow is shallow and tends to fade posteriorly; border is narrow and rather flat but increases slightly in size around the posterior end; ornament consists of granules like those on the cephalic doublure.

Thorax of 11 segments; axis tapers slightly from 1st to 6th or 7th segment, then a little more abruptly; width of last ring is about three-quarters width of first; rings are moderately arched; lateral nodes are clear, defined in front by a wide, shallow notch; notches clearly join to isolate the node. Adaxial (horizontal) part of pleura is narrow (tr.), only about one-third the width of the corresponding axial ring; height of vertical part of pleura of first segment is twice the width of the horizontal part and remains more or less the same on all segments. Posterior edge of posterior band has a strong articulating flange that fades away abruptly at the fulcrum; anterior edge of anterior band has a shallow articulatory furrow that extends laterally beyond the fulcrum down the leading edge of the facet. Pleural furrow is deep, long (exsag.), and very oblique, running from the anteromedial corner of the pleura and fading away on the upper part of the facet. Pleural end on last segment has an acute anteroventral tip, from which the posterior edge of the facet swings up in a broad arc; anteroventral tip on more anterior segments becomes progressively closer to a right angle, and the arc forming the posterior edge of the facet becomes progressively tighter; pleural extremities are notched to fit the vincular notches.

Doublure on pleural ends is more or less quadrangular, highest on 5th or 6th seg-

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[1] See Struve (1958, p. 167) for symbols.

ments and diminishing to about three-quarters of this value on the 1st and last segments; panderian notches are shallow, open, and more or less symmetrical; on the more posterior segments the panderian protuberances become lower (in a vertical sense) and progressively more pronounced, and the articulatory notches, into which they fit, become progressively less pronounced.

Pygidium is squat, with length/width averaging 3/5; in lateral profile the ventral edge is horizontal and the crest of the axis is inclined at about 40°; in posterior profile, anterior ring is highly arched, and more posterior rings are progressively less so; emargination at posterior extremity of margin is slight; width across the fulcral points is 1.6-1.8 times the width of the 1st ring; 7-8 axial rings plus a terminus, with 1st (and sometimes 2d) ring disproportionately wide, showing a vague lateral node and extending out to interrupt the axial furrow; subsequent rings are truncated laterally and drop vertically into the continuous axial furrow; 1st, 2d, and sometimes 3d and 4th rings have narrow, short pseudo-half rings; last 4 rings are very short (sag. and exsag.) and have a narrow median part that is flexed forward. Apodemal muscle scars are in two sets: (a) a main adaxial one on faint forwardly convex arcuate ridges, slightly stronger at their inner ends; and (b) a low, rounded node at the end of each of the first three axial rings being confluent. Seven (occasionally 6 or 8) pleural furrows usually can be seen, the last 1 or 2 indistinct; pleural furrows are deep, with equal slopes front and back, and fade away well inside the margin; first 5 interpleural furrows are clearly defined, but subsequent furrows become indistinct; these fade not only laterally but also adaxially and do not reach the axial furrow. Border is not defined, but there is a narrow rim, marked off by dense, fine ornament. Doublure consists of a narrow, slightly inclined outer band and a much wider vertical inner band, separated by a sharp junction; neither band contracts at the posterior extremity, but the sharp line of junction does disappear on some specimens; anterolateral corner of doublure has a slight articulatory notch.

Ornament consists of granules over almost the entire surface except the furrows; a few weak tubercles are present on the first 2 or 3 axial rings; a narrow, rather smooth band is present just above the margin.

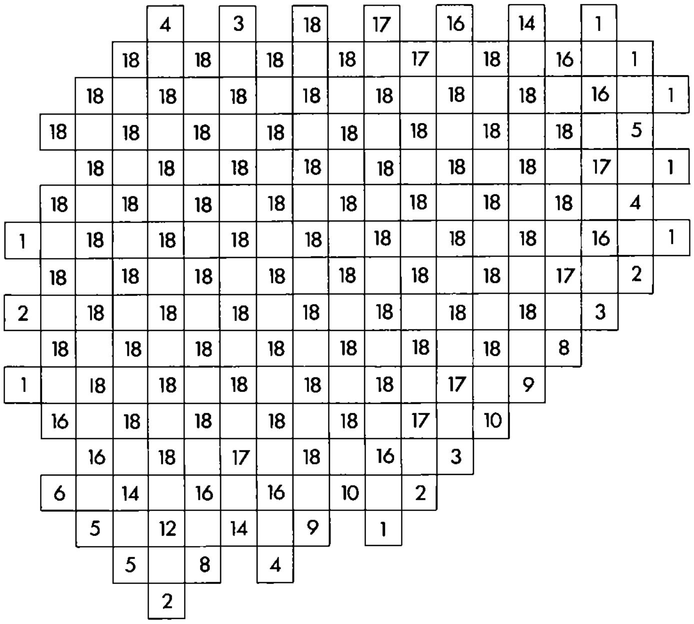
Large-eyed form

Description.—(This is written in comparative form to avoid duplication.) Maximum/minimum glabellar width 8/5; glabellar length/glabellar width averages 1.04 (range 0.95-1.10); axial furrows are shallower and wider, slope gradually up to both the glabella and the palpebral area, and diverge forward at 45°-55° in front of 1p; in lateral profile, glabella is less inflated in front; occipital ring is moderately high and has a median tubercle of variable strength; occipital furrow is much shallower; lobe 1p is not much lower than the occipital ring and continues the profile of the anterior part of the glabella; lateral nodes of 1p are more transverse in outline and are separated off by much weaker notches; furrow 1p is more slit-like and discontinuous medially. Posterior border furrow is longer, with a sloping rather than vertical front wall, and with a rounded or slightly flattened floor. Palpebral area is proportionately wider (tr.), palpebral lobe proportionately narrower, palpebral furrow less deeply incised both anteriorly and posteriorly; rim on palpebral lobe is less thickened and in lateral profile has a low point above file 8; palpebral lobe is downturned only slightly laterally.

In anterior profile, visual surface is slightly convex and is inclined at 8°-12° to the vertical; in plan view, curvature increases posteriorly; total number of lenses 80-116 (average 98) in 16-19 (a strong mode at 16, one specimen at 19) files; typical arrangement 567 777 776 766 554 3; statistical pattern is as shown in text-figure 12; lenses are tightly packed, with the distance between centers of adjacent lenses in a file averaging 0.4 mm in adults; diameter of largest lenses is approximately 0.3 mm; sclera lies well below the level of the lenses and is best developed in the upper part of the eye, where it shows faint granulation on well-preserved specimens.

Post-ocular part of fixed cheek is rather flattened and grades evenly into the palpebral area; $\frac{H}{A}$ varies from 0.24 to 0.34 (average 0.28), and $\frac{A}{G}$ from 0.44 to 0.50 (average 0.48). Posterior limb of facial suture is in a slight postocular furrow and forms a tight arc across the border furrow and the inner part of the border.

Ornament of occipital ring (including lateral nodes) consists of 8-12 low tubercles on



Text-figure 12. Statistical pattern of lenses in 18 specimens of large-eyed *P. (Paciphacops) raymondi* (Delo) from Haragan Formation at Old Hunton Townsite and White Mound. See explanation of text-figure 11.

each side of the median node, with fine granules in clusters on the tubercles and more sparsely between them; lobe 1p has a similar pattern, though with fewer granules between the tubercles; remainder of glabella has granule-crested, scattered tubercles that increase in density toward the front; granules are present between the tubercles on the anterior slope; anterolateral corner of glabella has granules only; all glabellar tubercles have a strong axial perforation; posterior border has same type of ornament as occipital ring, and palpebral area and lobe have same type as posterior part of glabella; palpebral rim and lateral and anterior borders have granules only; all granules are much finer than those on small-eyed species.

Median length of doublure (measured from posterior edge of vincular furrow) is about 0.30 times total glabellar length; vincular furrow is slight but is distinct around the anterior of the cephalon; laterally, inner wall of vincular furrow fades abruptly, forming an asymmetrical furrow that is only faintly notched, if at all; doublure and furrow are ornamented with granules occasionally arranged in lines laterally.

In thorax horizontal part of pleurae is slightly wider proportionately. Ornament of rings consists of a variable number of scattered tubercles of variable size (correlated with the ornament of the occipital ring) and a complete covering of granules; horizontal part of both anterior and posterior bands rather is smooth, witth a few granules developed laterally; downturned part of posterior band is densely granulose and in many specimens carries tubercles that diminish in size and number ventrally.

Pygidium in lateral profile shows crest of axis inclined to the horizontal at about 25°-30°; in posterior profile axis is highly arched; width across fulcral points measures 1.8-2.6 times width of first ring; axis is narrow and slightly constricted in outline; 9-10 axial rings plus a terminus; 8 or 9 pleural furrows can be seen, the last 2 or 3 somewhat indistinct. Ornament consists of rings similar to that of thoracic rings; anterior and posterior bands of first 5 or 6 pleurae each bear a row of low tubercles that fade toward the border.

Remarks.—The holotype of this species is a large-eyed cephalon with a subtriangular outline to the anterior part of the glabella. Undistorted specimens show a rounded to faintly subtriangular anterior outline, and hence I regard the glabella outline figured by

Delo as being either at one extreme of the variation range or a slightly distorted specimen. It remains true, however, that the large-eyed morph sometimes has a slightly more angular glabella than most other members of the genus. Of the other diagnostic features mentioned by Delo, only the narrow vincular furrow and the narrow pygidial axis are of significance. His statement that there are no distal "knots" on the thoracic rings is not correct.

It should be noted that the counts of the lenses in the large-eyed morph given herein are different from those given by Eldredge. I have seen no specimens with a count as low as 67, and although there is no clear mode in my sample, half the individuals have 100 or more lenses, whereas only one-sixth of his specimens fall in this range. I am at a loss to understand this discrepancy. It cannot be explained by our sampling of different localities, because there appears to be no difference between the populations at White Mound and Old Hunton Townsite. Nor is it the result of differing specimen size. Our samples cover almost the same size range, though I have not counted an individual with cephalic length of more than 12 mm.

Eldredge (1973) has made a good case for the close relationship of *P. raymondi, P. logani* (Hall), and *P. birdsongensis* (Delo), and he has, in fact, considered them to be subspecies of *P. logani* (see discussion under the subfamily). I am not convinced, however, that all three forms are morphologically more similar to one another than they are to any other known form. Moreover, for reasons set out below, I cannot accept the view that *raymondi* is more closely related to *birdsongensis* than either is to *logani.*

It is certainly true that in both numbers of lenses and files the small-eyed *raymondi* is closer to *birdsongensis* than it is to the silicified specimens of *logani* described herein, but Hall's type *hudsonirus* (presumably a small-eyed *logani*) is quite similar to both *raymondi* and *birdsongensis*. It seems probable that there is some variation in small-eyed *logani* that has not shown up because of inadequate sampling.

Our sample of large-eyed *logani* is not large enough to be statistically significant (see description below). Judging from Eldredge's sample, *logani* overlaps *raymondi* almost completely in total lens number, but they have modes of 17 and 16 files, respectively. On the other hand, *birdsongensis* resembles *logani* in the number of files, but it has consistently fewer lenses than either *logani* or *raymondi.*

The factor analysis undertaken by Eldredge (1973, figs. 16, 17), which took into account cephalon size, number of files, and total number of lenses, showed the uniqueness of the large-eyed *birdsongensis* populations, as well as the large overlap between the *raymondi* and *logani* populations. It would seem to be impossible, therefore, to ally *raymondi* with *birdsongensis* on the basis of these quantitative aspects of eye morphology. It is more likely to be related to *logani* if the factor analysis is accepted. This conclusion would be strengthened if the values for the lens counts in *raymondi* given herein were used, rather than the lower values used by Eldredge. However, he concluded that "although eye morphology and polymorphism offer good criteria to add to the diagnoses of *P. l. raymondi, P. l birdsongensis* and *P. l. logani,* the relationships among the subspecies are more appropriately assessed on other criteria" (p. 308). The reasons for this are not clear to me.

One of these other features that seems to me to be consistent within a group is the nature of the sclera between the lenses. Large-eyed *logani* and *birdsongensis* have a thick, inflated sclera, whereas *raymondi* has relatively large lenses protruding well above a narrower sclera. The possibility that the closest relationship is between *logani* and *birdsongensis* was found to be supported by several other features, almost all of which are concerned with dimorphism. In almost every instance it is the large-eyed *raymondi* that exhibits some peculiarity, just as it does with the sclera. The following is a list of the features in which it is distinctive.

1. Lobe 1p is not depressed far below the general curve of the glabellar profile, its lateral nodes are transverse in outline, and the notches separating off the nodes are weak.

2. The axial furrows on the cephalon in front of 1p are unusually shallow and are divergent at a reduced angle.

3. The posterior limb of the facial suture has an unusually sharp flexure across the border furrow.

4. The vincular furrow is distinctly re-

duced anteriorly, the inner wall of the furrow is modified (see description for details), and there are a few weak lateral notches.

5. The number of axial rings is 9 or 10 plus the terminus, and there are 8 or 9 pleural furrows. Corresponding figures for the small-eyed form are 7 or 8 plus the terminus, and 6-8 pleural furrows. *P. birdsongensis* and *P. logani* show no pygidial dimorphism.

One final piece of evidence concerns the form of the hypostome. This structure is known from the large-eyed *logani* and *birdsongensis* and the small-eyed *raymondi*. In the two former species its proportions, furrows, borders, and spines are closely comparable, whereas in *raymondi* the convexity of the hypostome is greater, it is proportionately narrower posteriorly, the border furrows are not so strongly impressed, and the border is less pronounced. Some of these differences may be due to dimorphism, but it is difficult to believe they all are. In any case, *birdsongensis* and *logani* are shown to be closely comparable in all characters except the lateral outline, which is more curved in *birdsongensis*.

The only features in which *birdsongensis* is more closely related to *raymondi* than to *logani* are (a) the absence of the genal spine, or its reduction to a genal node; and (b) the "nearly 50-50 ratio of small-eyed versus large-eyed forms" (Eldredge, 1973, p. 310). The first feature is also shown by some specimens of *logani,* and the significance of the latter feature is dubious because of sampling and preservation difficulties. In any case, these features are not of sufficient moment to outweigh the previously mentioned considerations.

In order to explain the development of these relationships, one would have to postulate that *raymondi* had become isolated from the *logani-birdsongensis* complex by some geographical barrier or by an interval of time.

Material.—The holotype has been lost. The above description is based on more than a hundred specimens, mainly from the Old Hunton Townsite and White Mound localities, now housed in the Oklahoma Geological Survey and U.S. National Museum collections.

Paciphacops (Paciphacops) logani
(Hall, 1861)
Pl. 12, figs. 1-4; pl. 13, figs. 3, 4

(For synonymy, see Eldredge, 1973, p. 296.)

Material.—The Helderberg material available to me is limited to 12 incomplete and poorly preserved specimens from "Clarksville" that are in a black, partly dolomitized limestone, probably the Kalkberg; and about 30 silicified specimens, including 8 almost complete cephala, 10 almost complete pygidia, and 10 isolated thoracic segments, from "Indian Ladder" in the John Boyd Thatcher State Park, probably from the New Scotland. Both these collections are from the Yale Peabody Museum Beecher Collection. The former is unnumbered; the latter is all under the number 6595. In addition, Dr. Eldredge has kindly provided me with latex casts of the types of both *P. logani* and *P. hudsonicus*.

The Clarksville material contains at least 3 specimens with large eyes and possibly 2 with small eyes. All the Indian Ladder specimens are of the small-eyed type. This is of considerable importance, because Eldredge was able to find only 2 small-eyed types in his collection of 150 specimens of the species. For this reason this morph is described in detail, and the large-eyed one, in comparative terms only. The description is based mainly on the Indian Ladder material, but all available specimens have been used.

Small-eyed form

Description.—Largest specimen has a glabella 13.8 mm long; maximum/minimum glabellar width is about)/1, and maximum glabellar width about 0.6 times total width of cephalon. Forward of furrows 1p, axial furrows diverge at 75°-80°; axial furrows are deep, with the wall against the glabella steeper than that against the cheek. Glabellar shape is as in *P. raymondi*. Occipital ring has a small node placed medially rather than posteriorly, and apparently never developed a triangular posterior profile for the ring; lateral nodes are poorly defined and not inflated. Occipital furrow is rather longer (sag. and exsag.) than that of *P. raymondi*. Lobe 1p has sharply separated globular lateral nodes; median part is slightly depressed; furrow 1p in some specimens is incomplete, being broken by normal glabellar ornament, but in most specimens it is complete, though definitely reduced axially. Furrows 2p and 3p are as in *P. raymondi*. Shape of posterior border and border furrow is as in *P. raymondi;* genal angle is bluntly rounded and without a genal node. Palpebral furrow is distinctly curved, deepest posteriorly, shallowest medially, and deepens only slightly anteriorly. Palpebral area, lobe, and rim are as in *P. raymondi*. Eyes consist of 46-57 (average 54) lenses arranged in 16 or 17 files, with a strong mode at 16; typical arrangement is 234 444 343 443 433 2; distance between adjacent lenses in a file is 0.60 mm, with maximum lens diameter 0.30 mm in a specimen of glabellar length of 13 mm; sclera appears to be slightly below to slightly above the general level of the surface of the lenses; internal structure of lenses is not known. Subocular region is concave. Postocular part of fixed cheek, shape of posterior limb of facial suture, and values, all are as in *P. raymondi* small-eyed morph.

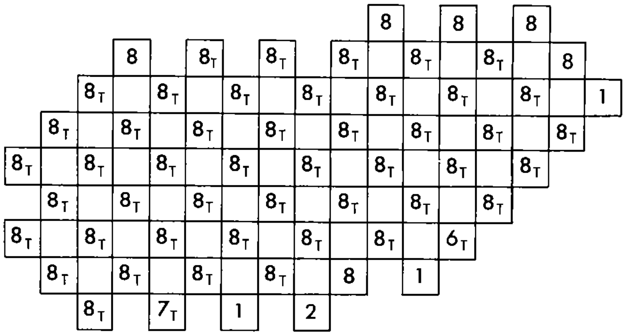
Median length of doublure measures 0.24-0.28 times total glabellar length; vincular furrow is strong around the whole cephalon; laterally, the inner wall is sharply truncated opposite the end of the posterior border furrow; vincular furrow has 9 clear notches and a scarcely visible 10th, indicating that all thoracic segments had interlocking tips. Hypostomal suture is as in *P. raymondi*. Ornament of doublure consists of very fine granules (much finer than in *P. raymondi*) and shows little suggestion of linear arrangement laterally. Hypostome is not known.

Pygidium is squat, with length/width ratio about 1:2; width across fulcral points measures about 1.8 times width of first ring. There are 8 rings plus a terminal piece, with the 8th sometimes incomplete axially; rings form broad arches, much flatter than those of *P. raymondi;* narrow pseudo-half rings are present on 1st 3 segments, the 3d one being barely visible; other features of rings are as in *P. raymondi*. Number and shape of pleurae, pleural furrows, and border are as in *P. raymondi*. Outer band of doublure has a slight furrow parallel to the margin and is separated from the inner band by an obtuse angular junction; steep inner band has a slight axial emargination. Ornamentation is weak, consisting of a few vaguely defined nodes on the rings and pleurae of some specimens; others apparently are almost smooth; granulation is weak to absent.

Large-eyed form

The following is a list of the characters in which the large-eyed differs from the small-eyed form.

1. The axial furrows in front of 1p are somewhat shallower, and diverge at 75°-80°.
2. The palpebral lobe is high and not turned down laterally.
3. The lens pattern is as shown on text-figure 14. The sclera is invariably strong. The largest lenses are about 0.35 mm in diameter, and the centers of adjacent lenses in a file are 0.50 mm apart in a specimen of glabellar length 11.5 mm.



Text-figure 13. Statistical pattern of lenses in eight specimens of small-eyed *P. (Paciphacops) logani* (Hall), probably from New Scotland Formation, Indian Ladder, Helderberg Mountains. *T* represents lenses present in type specimen of *Phacops hudsonicus*. There is a possibility of small lenses at dorsal end of one or more of files 11, 13, 15 and 16 of this specimen. See explanation of text-figure 11.

4. The genal angles bear either a node or a short spine.

5. The intercalating ring has more tubercles.

6. The tubercles on the composite glabellar lobe have a large axial perforation, and the superimposed granules tend to become slightly coarser and more numerous on the anterior slope of the glabella.

7. The vincular furrow is possibly a little less strongly notched laterally.

8. The sclera in the eyes is not as thick or as high with respect to the lenses, but it is much thicker than that in the large-eyed *raymondi*.

9. The tubercles on the occipital ring and the axial rings of the thorax are stronger. These tubercles also are distinctly perforate.

As far as I can determine from the limited material available, all other characters are similar.

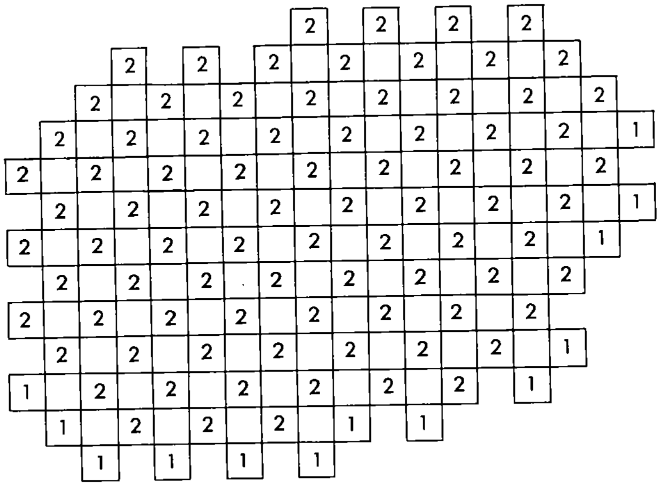
One Clarksville specimen has the internal mold of a hypostome preserved almost in position. As this structure is inadequately known, it is described using this specimen and the fragment figured by Eldredge (1973, fig. 1i).

Hypostomal suture is concave; lateral margins are almost straight and convergent; width across posterior extremity measures about 0.4 times width across anterior edge (excluding anterior wings), which is about 1.1 times the length (sag.) of the hypostome; border is narrow and convex throughout, but widens slightly at the anterolateral corners; posteriorly, border is produced into a pair of short, sharp lateral spines and a blunt median projection; in posterior profile middle body is highly convex, and in lateral profile it has a shallow furrow between the maculae and a pronounced hump behind; maculae are strong on the internal mold and are situated well in front of the posterior wings; width across anterior wings measures 1.5 times width without wings; ornament is granulose.

Remarks.—The preservation of the Clarksville specimens makes possible certain observations about the morphology of the internal surface of the exoskeleton. The perforations in the tubercles of the large-eyed morph are surrounded by rims of the same type as those in the dalmanitids described below. Between these there are smaller rims of similar structure. These are not as closely spaced as the granules that cover the surface, and they appear to be absent on the flanks of the tubercles. Either they are quite unrelated to the granules, or they occur in only a limited number of them. They are also present on the borders and at least the anterior part of the doublure.

Structures of this type have been recorded in thin section by Dalingwater (1973), who figured them in a specimen of *Illaenus aduncus* Jaanusson (pl. 108, fig. 3). Their significance is unknown.

The type specimen of *P. hudsonicus* Hall (the small-eyed morph of *logani* as was shown by Eldredge) and the second specimen measured by Eldredge have fewer lenses



Text-figure 14. Statistical pattern of lenses of large-eyed *P. (Paciphacops) logani* (Hall). The 17-file specimen is NYSM 13885/3, figured by Eldredge (1973, figs. 1a-c). The 18-file specimen is AMNH 2612/1. Information supplied by Dr. Eldredge.

than the specimens from Indian Ladder, but except for that there is little reason for separating the two populations. The number of files is the same. It may be important that the Indian Ladder specimens are close to the intermediate morph of *birdsongensis* in eye structure. On the other hand, the preservation of the type of *hudsonicus* is far from perfect, and the possibility of the presence of small lenses at the top of one or more of files 11, 13, 15, and 16 cannot be excluded, at least in the cast available to me. In that case, this specimen may be closer to the Indian Ladder specimens than text-figure 13 suggests.

Paciphacops (Paciphacops) birdsongensis (Delo, 1940)

Pl. 9, fig. 4; pl. 11, figs. 1, 2; pl. 13, figs. 5-7

Phacops logani var. *birdsongensis* DELO, 1940, p. 19, pl. 1, figs. 13-15.

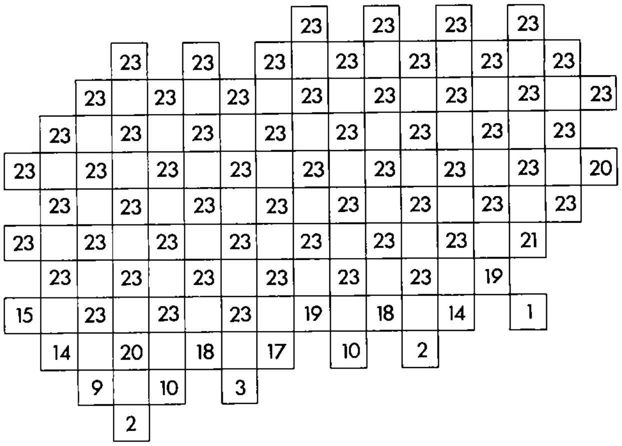
Phacops logani birdsongensis Delo; ELDREDGE, 1973, p. 296-297, fig. 2.

Material.—About 40 specimens including 25 with measurable eyes, USNM 136977, 27849, 27850, from the Birdsong Shale near the Steel Bridge over Big Sandy River, Benton County, Tennessee. It is not known how these specimens were related to one another in the field. A Memphis State University collection made by Prof. L. G. Walker, from measured intervals in the top 15 feet of the Birdsong Shale, contained 7 specimens with measurable eyes and 15 others for which the eye type could be identified but not measured in detail. Another small MSU unlocalized collection, probably from similar levels, contains four measurable eyes. In addition, 11 specimens from the Ross Formation at Pickwick Dam, USNM 94592 and 144308, have been available for study.

Remarks.—There is an obvious general similarity between this species and *raymondi*, and Eldredge (1973) regards them as sister species. Girty (1899) and Tansey (1922) both referred specimens of this species to *P. logani* and *P. hudsonicus,* noting that they may be dimorphs of the one species. Delo (1940) believed that the number of lenses in the eye indicated the possibility of three groups within the species. Eldredge (1973), using much more material and more sophisticated methods, supported this conclusion. He had 59 specimens from a number of localities and "beds," though most were from the "trilobite zone" of the Birdsong Shale. From a study of three variables, i.e., number of files of lenses, total number of lenses and cephalic length, he concluded that 3 specimens from a measured sample of 25 (see his fig. 8) formed an intermediate group between the normal large- and small-eyed morphs, each of which numbered 11. Subsequent factor analysis showed some ambivalence in the relationship of these 3 specimens, but he concluded that the presence of a 3d discrete morph was a definite possibility and that "Delo's (1940) observation that there seems to be intergradation between a *logani* and a *hudsonicus* eye type within the Birdsong *Phacops* is confirmed quantitatively."

The following conclusions about the variation in eye morphology have been derived from the present study.

1. There is a clearly definable large-eyed type, almost all specimens of which have 17 files. Eldredge (1973) reported 1 specimen with 19 files. The bulk of the specimens from Big Sandy River, probably about 80 percent, and all those from Pickwick Dam, belong to this group. Eldredge's sample contained only about 50 percent of large-eyed types.
2. The controlled collection made by Professor Walker consists of large-eyed types, with one possible exception.
3. The Big Sandy River and Pickwick Dam collections cannot be distinguished on lens counts.
4. The remainder of the collection from Big Sandy River contains specimens with 14 or 15 files, the number being independent of specimen size.
5. As shown in text-figures, 16 and 17, with only one exception the specimens with 15 files have 3 or 4 lenses in files 2 to 10, whereas those with 14 files have only 2 or 3 lenses in these files.
6. This differentiation between specimens with 14 and 15 files shows up also in total lens number. Those with 15 files have 40-48 lenses, with 1 exception having 33 lenses. Those with 14 files have 31-35 lenses. This difference cannot be explained simply by the addition of another file, because the maximum in any file is four lenses. These data conflict with those given by Eldredge in table 2. Total lens numbers in 14-file forms from his sample are 33 to 39, and in 15-file forms



Text-figure 15. Statistical pattern of lenses in 15 specimens of large-eyed *P. ((Paciphacops) birdsongensis* (Delo) from Birdsong Shale at Big Sandy River, and 8 from Ross Limestone at Pickwick Dam. Small numbers at ventral ends of files 4, 7, 12, and 15 are contributed by Birdsong specimens. See explanation of text-figure 11.

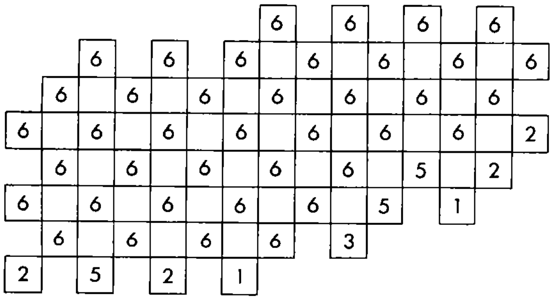
39 to 49 (one with 55), thus making a transition between the two. However, even on these data there is no overlap between the 14- and 15-file forms, or between the 15-file and the large-eyed 17-file forms.

It is clear, therefore, that on eye morphology alone, three distinct morphs can be recognized as shown in the next column:

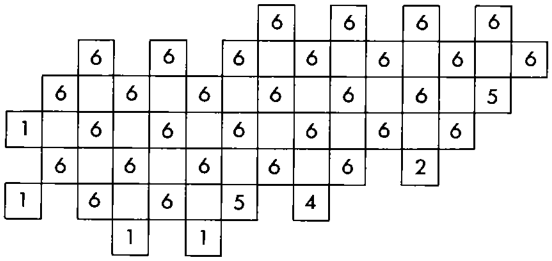
No. of files	Total lens number	Mean lens number
14	31-39	34
15	39-55	44
17	63-83	72

There are other distinct differences between the 17- and 14-file forms, as shown in the following table:

Morphology	17-file forms	14-file forms
Occipital ring	Without median tubercle	With large median tubercle on 80 percent of specimens.
Occipital and pygidial thoracic ring ornament	Scattered low tubercles with granules on and between them.	Granulate with tubercles rare or absent.
Lobe 1p	Few tubercles, lateral nodes strong.	Many tubercles, lateral nodes strong.
Tubercles on composite lobe	Scattered, some intermediate secondary tubercles, large ones coarsely perforate.	Closely packed, numerous intermediate secondary tubercles, large ones not coarsely perforate.
Glabellar granulation	Covering most tubercles, but absent between them.	Present on and between most tubercles, but more concentrated on front of composite lobe.
Palpebral lobe and rim	Slightly downturned laterally.	Strongly downturned laterally.
Palpebral furrow	Shallow at mid-length.	Deeper at mid-length.



Text-figure 16. Statistical pattern of lenses in six specimens of intermediate (15-file) morph of *P. (Paciphacops) birdsongensis* (Delo) from Birdsong Shale at Big Sandy River. Small numbers of ventral ends of files are contributed by same specimens. See explanation of text-figure 11.



Text-figure 17. Statistical pattern of lenses in five specimens of small-eyed (14-file) morph of *P. (Paciphacops) birdsongensis* (Delo), and one 15-file morph of same species, from Birdsong Shale at Big Sandy River. The 15-file specimen is aberrant in that it has less than normal number of lenses in each file. See explanation of text-figure 11.

The intermediate, or 15-file, morph is closer to the large-eyed one in all these characters except the shape of the palpebral furrow. Thus, there is a peculiar situation in which this morph is closer to the small-eyed morph in eye characters and to the large-eyed one in others (see comments on p. 10).

The species may be distinguished from *P. (P.) raymondi* in the following ways.

1. The lens counts are different, as was shown by Eldredge (1973) and as is confirmed by the present study.
2. The sclera in the large-eyed morph is thicker and higher with respect to the lenses than that of *raymondi* and is covered with granules.
3. It does not show the axial furrow or the pygidial dimorphism of *raymondi*.
4. The vincular furrow in all three eye types is distinctly notched, whereas in *raymondi* the large-eyed morph is only indistinctly notched.
5. There is no median occipital tubercle in the large-eyed morph.

Fittstown Member occurrences.—A single cephalon, OU 7211 (pl. 15, fig. 3) from Amsden collecting locality P16, which is at the top of the Fittstown Member, cannot be distinguished from the large-eyed morph of *P. (P.) birdsongensis* in eye morphology, structure of the occipital and 1p lobes and furrows, and postocular characters. However, it has only a few weak tubercles on the palpebral area, and there is almost no granulation on the tubercles of the posterior half of the glabella. It is herein referred to as *P. (P.)* cf. *P. (P.) birdsongensis*.

Cravatt Member occurrences.—Several poorly preserved specimens from the Cravatt Member are more closely related to *birdsongensis* than to any other described form. Two of them, OU 8286 and 8274, have eyes that can be counted, and they have 17 files, with a maximum of 5 lenses per file and a total of 63-65. The sclera is thick and high, and the intercalating ring is well developed. The ornament is not well preserved on any specimen. In addition, there is a small-eyed morph, OU 8288, with 14 files and a lens pattern close to, or identical with, that of the small-eyed *birdsongensis*. It is certainly different from *raymondi*.

OU 8285 is from Amsden collecting locality Cal$_{(1)}$-X; OU 8286 from Cal$_{(2)}$-S2; OU 8287 from M11-E; OU 8288 from P9-0; and OU 8274 from C1-P.

Paciphacops (Paciphacops) invius,
new species

Pl. 14, fig. 2; pl. 15, figs. 1, 2, 7

Type.—Holotype OU 7213 from the Fittstown Member, Henryhouse Creek, SE¼ sec. 30, T. 2 S., R. 1 E., Carter County, Amsden collecting locality Cal$_{(2)}$-V2.

Diagnosis.—Large-eyed morph with lens pattern like that of *raymondi*. Axial furrows diverge at 65° in front of 1p; lateral occipital lobes are demarcated by shallow furrows that extend to the posterior margin; lateral parts of lobe 1p are sharply differentiated and intercalating ring is high and strong; median tubercle lies on occipital ring; small genal nodes are present; glabella, lobe 1p, and occipital ring have tubercles 0.3-0.6 mm in diameter, with smaller ones between, especially on the front of the composite lobe; granules are present only on tubercles on the anterior face of the composite lobe; there are small tubercles on the palpebral area, on the palpebral rim, and on the genal region of the posterior and lateral borders; these and the glabellar tubercles are coarsely perforate; remainder of dorsal surface is sparsely to densely granulate, except for the lateral part of the lateral borders, which has faint irregular ridges; vincular furrow is strong and continuous but is only faintly notched laterally; hypostomal suture is wide and transverse; ornament of doublure is granulate.

Remarks.—The holotype is the only definitely assigned cephalon available. A second cephalon, OU 8260, from Amsden collecting locality P3-JJ almost certainly belongs to the species, but its eyes are not preserved. The morph is readily distinguished from the large-eyed *raymondi* by its occipital node, its glabellar profile, and the more transverse glabellar outline, though *raymondi* is obviously its closest described relative. The species shows an advance toward *cristata* in the reduction of the granulation on the glabella to the anterior face of the composite lobe, but, on the other hand, there is no reduction in the strength of lobe 1p or in the number of files in the eye.

There is a well preserved pygidium, OU 7214, from the Fittstown Member at Buckhorn Ranch, SW¼SE¼ sec. 33, T. 1 S., R. 3 E., Murray County, Amsden collecting locality M10-P. Its size and ornament suggest that it is the pygidium of this species. Its description is as follows.

Pygidium is highly arched; axis tapers gradually and has a well-rounded terminus; 9 axial rings are present, plus a terminus; axial furrow is not well defined opposite first ring but becomes deeper opposite rings 2-5 and then fades slightly to the terminus; first 5 interpleural furrows are sharply defined, but the others are obscure or absent; 8 or 9 pleural furrows are visible, the most anterior ones sharply incised and with similar slopes front and back; anterior and posterior pleural bands are of approximately equal length; pleural furrows terminate at the inner edge of a wide border differentiated by an almost imperceptible border furrow; at least the first 4 interpleural furrows can be seen vaguely on the border. There are 4 to 6 weak, perforate tubercles on each of the 1st 6 axial rings, a few even weaker tubercles on both the anterior and posterior pleural bands of the pleurae, and scattered granules on the border, especially on the posterior part and the margin.

Probable small-eyed morph

Three small specimens that clearly belong to the same species may be the small-eyed morph of *P. (P.) invius*. One of them, OU 8261, comes from locality P3-JJ, the locality at which the second specimen of the large-eyed morph occurs. The other two, OU 7212A-B, are from the same section at locality P3-GG. All three specimens are characterized by an occipital ring that is ogival in posterior view but that has weakly differentiated lateral nodes; lateral nodes of lobe 1p are globular; intercalating ring is weak, and furrow 1p is poorly defined medially; axial furrow is wide, deep, and continuous into the well-defined preglabellar furrow; palpebral area is small and palpebral lobe wide; eye has 15 files, (1 possibly has only 14), with a maximum of 5 lenses per file, and a total of 50-56; a broad convex band is present beneath the eye; sclera is thick and high; vincular furrow is clearly defined anteriorly and strongly notched laterally; glabellar ornament consists of crowded depressed tubercles, with a few superimposed granules on the anterior ones.

Remarks.—The occurrence of one of these specimens with a probable *P. (P.) invius,* plus the general similarity of their glabellar ornament, suggests that these are the small-eyed morphs of the species. They differ from the intermediate *birdsongensis*, which also has 15 files, in the glabellar ornament. The eye counts of all three are slightly different as far as can be determined, but this is considered to be natural variation.

Paciphacops (Paciphacops), new species
Pl. 15, figs. 5, 6

Material.—OU 2002A-B from the Frisco Formation, NE¼SE¼ sec. 7, T 1 N., R 7 E., Pontotoc County; 5 feet above base of Ventress' Section 3, Canyon Creek Ranch. OU 8263 from north of Coal Creek, NW¼ sec. 22, T. 1 N., R 7 E., Pontotoc County, Amsden collecting locality P9-R.

Description.—Glabella is moderately convex; anterior face of composite lobe is vertical to slightly overhanging the anterior margin; occipital ring is highly arched, without a median node; lateral lobes of lobe 1p are short and low; median part of lobe 1p is clearly defined, but short and not depressed; axial furrows diverge at about 70° in front of 1p; palpebral furrow is continuous across the palpebral area, and makes only a shallow postocular depression; palpebral lobe is downturned all around its margin; eyes have 15 files of lenses, with a maximum of 5 (possibly 6 in 1 specimen) in a file, totaling 67; lens count (front to back) is 345 555 555 545 432; sclera is unknown; deep concave depression lies beneath eyes; genal angle has no spine; vincular furrow is continuous, very narrow, and notched laterally; hypostomal suture is transverse and straight to slightly convex; ornament of composite lobe is tuberculate, with internal molds showing collars around perforations in their axes; weaker tubercles on palpebral areas and flanks of occipital ring are also perforate; doublure has discrete granules all over, lateral granules show a suggestion of linear arrangement.

Remarks.—This species is represented by three incomplete cephala, none of which has the external surface of the composite glabellar lobe preserved. Thus, important details of the ornament are unavailable. Small areas of the occipital ring and the palpebral area, however, show no granules or tubercles.

The intermediate morph of *P. (P.) birdsongensis* has 15 files, but the total number of lenses and the maximum number per file is smaller. The closest described form is the *Phacops logani* subspecies A of Eldredge (1973, p. 301) from the Becraft Formation of New York. They both have 15 files and similar numbers of lenses in the eyes, though it could be argued that the 67 in the Frisco form may prove to be significantly less than the 73 in the Becraft. Both have the intercalating ring reduced, though the Frisco specimens are even more reduced than the Becraft. Indeed, they are so far reduced that only 1 row of 2-4 tubercles occurs on it. Another significant difference is that tubercles of only one size occur on the composite lobe of the Frisco specimens, and all of them are punctate. The axial furrows of this form also are more strongly divergent. For these reasons, I consider the Frisco specimens to be more advanced, and in most respects they seem to have reached the level of *P. (Viaphacops)*. The axial furrows, however, have not reached the angle of divergence, nor is the ornament of the doublure sufficiently linear, to regard the species as a typical member of that subgenus. It seems to me to be a true intermediate.

Paciphacops (Viaphacops)
Maksimova, 1972

Type species (by original designation).—*Phacops pipa* Hall and Clarke (=*Phacops cristata bombifrons* Hall *fide* Eldredge, 1973, p. 315) from the Onondaga Limestone of New York.

Diagnosis.—Moderate size for subfamily. Glabella is moderately to strongly inflated, and its front wall varies from vertical to markedly overhanging the anterior border; axial furrows diverge at 75°-90° in front of lobe 1p; lateral lobes of lobe 1p are depressed and short (exsag.), and intercalating ring is weak or is almost incorporated in the back of the composite lobe; glabellar ornament consists of tubercles of one or two orders intermingled bt with little change in dimensions or shape from back to front; large central perforation is usually present in largest tubercles; granulation is superimposed only on scattered tubercles at the anterolateral extremities; eye has 13-17 files and thick, raised sclera; weak to strong braided ornament occurs on the lateral border; doublure has granules medially that in some specimens become arranged into weak terrace lines laterally; vincular furrow is continuous, notched laterally; hypostomal suture is straight to concave; pygidium has 6-9 axial rings plus a terminus; there are clearly defined interpleural furrows on at least the first 4 or 5 segments; weak tubercles on the axial rings and pleurae; granules around the margin.

Remarks.—Dimorphism is not mentioned in the above diagnosis because not enough is known about it. Eldredge believes that the North American forms I would place in the subgenus are not dimorphic in the eye structure, and this may be true for all members. The hypostome also is too poorly known to be included in the diagnosis, but from the evidence of subspecies of *cristata*, it is thought to be the same as *P. (Paciphacops).*

Paciphacops (Viaphacops) cristata cf. **P. (V.) bombifrons** (Hall, 1861)

Pl. 15, fig. 4

Material.—OU 7215 from the Frisco Formation, north of Coal Creek, NE¼NW¼ sec. 22, T. 1 N., R. 7 E., Pontotoc County. Base of Ventress' First Measured Section.

Description.—This specimen has a glabellar length of 23 mm and a glabellar width of 25 mm. The angle of divergence of the deep axial furrows in front of lobe 1p is 80°-85°. In lateral profile, the glabella is highly convex and markedly overhangs the anterior border. The occipital ring is not completely preserved, but it must have been high, and the lateral occipital lobes were slight. Lobe 1p is reduced to two tubercles on the back of the composite lobe medially, and the lateral 1p lobes are low and transverse. The ornament on the posterior half of the composite lobe consists of large, flat, coarsely perforated tubercles without granulation. On the anterior half they seem to have been similar, but details are not preserved. The eye is badly distorted but contains 13 or 14 files with a maximum of 5 lenses in a file. The sclera is thick and prominent. The vincular furrow is continuous, but other details of the ventral surface are poorly preserved. The hypostomal suture is concave, as judged from the shape of its lateral edges.

Remarks.—This form is obviously a member of the *cristata* group, as can be seen from the glabellar outline and ornament, the reduction of lobe 1p, and the eye morphology. Without more data, assignment to a subspecies is impossible. However, ornament and glabellar and lobe 1p shapes indicate a relationship with *bombifrons* (Hall) or *gaspensis* (Clarke), which come from the Onondaga Limestone and Grand Grève Formation, respectively (Eldredge, 1973, p. 323, 329).

Paciphacops (Viaphacops), new species

Pl. 14, fig. 1

Material.—OU 7216, from the Frisco Formation, north of Coal Creek, NW¼ sec. 22, T. 1 N., R. 7 E., Pontotoc County. Amsden collecting locality P9-R.

Description.—Cephalon is transverse, the width being 2.0 times the median length; glabellar width measures 1.2 times glabellar length; in lateral profile, glabella is only moderately convex and does not overhang the anterior border; axial furrow is wide and deep, diverging at 90° in front of the lobe 1p. Occipital ring slopes steeply into the large occipital furrow; lateral occipital lobes are not isolated, giving a distinct, angular posterior profile; median node is distinct. Lateral lobes of 1p are remarkably depressed and transverse; intercalating ring is an extension of the composite lobe medially but is clearly defined by furrows 1p laterally. Posterior border furrow is shortest (exsag.) opposite the fulcrum, but lengthens only slightly away from this point, and junction with lateral border furrow is subrounded; lateral border furrow is wide and shallow, the shallowest point reached where it joins the axial furrow; a distinct rim is present around the lateral border.

Palpebral furrow is very faintly curved in plan view, merging gradually into the axial furrow; palpebral area is narrow and is inclined steeply down into the axial furrow; palpebral lobe is unusually wide and is set markedly above the palpebral area, slightly domed, and bounded by an unusually wide rim, inside which are a few shallow pits; palpebral lobe is almost semicircular in outline. The length of ϵ-ϵ is approximately equal to γ-γ, and each is somewhat less than the maximum glabellar width; ϵ-ϵ passes through the axial part of the occipital furrow. Visual surface of eye is distinctly convex in any vertical section; 15 files of lenses are arranged 334

343 444 434 332, giving a total of 51; lenses are set in massive smooth sclera; largest lenses measure 0.3 mm in diameter; distance between centers of adjacent lenses in a file measures approx. 0.6 mm, total length of visual surface 5.5 mm, and glabellar length 12.0 mm. Lower edge of visual surface is bounded by a faint groove, surmounting the steep and gently convex cheek, which reverses curvature and passes into the lateral border furrow. Postocular part of fixed cheek is strongly convex; sutural furrow is deep and continued onto the lateral border; genae are subangular and have a slight genal node, especially in juveniles.

Composite glabellar lobe is ornamented with low, rounded, coarsely perforated tubercles 0.3-0.7 mm in diameter, with scattered small tubercles between them; weaker tubercles are present on the flanks of the occipital ring, the intercalating ring, the palpebral area and lobe, and the genal region of the lateral and posterior borders; a group of granules lies in the anterolateral corners of the glabella, with rare granules superimposed on the tubercles, there are scattered granules on lateral border and beneath the eye.

Medial length of doublure measures about 0.25 times the glabellar length; vincular furrow is continuous, is well defined in front, and carries 9-10 notches laterally; hypostomal suture is distinctly concave; ornament consists of transverse granules medially, with granules organized to form irregular terrace lines laterally.

Remarks.—This form is placed in *P. (Viaphacops)* rather than in *P. (Paciphacops)* because of its weak lobe 1p, the absence of superimposed granules on the glabella, the development of incipient terrace lines on the doublure, and the concave hypostomal suture. Its transverse form, rather depressed glabella, and wide palpebral lobe distinguish it from any subspecies of *P. (V.) cristata.* In fact, there is no North American species with which it may be closely compared. The lens counts suggest some affinity with the intermediate *P. (P.) birdsongensis,* but almost all its other characters are against this.

In addition to the above specimens, there is a smaller one labeled OU 7217 from the Fittstown Member, Cedar Hill, SE¼ sec. 4, T. 2 N., R. 6 E., Pontotoc County, Amsden collecting locality P3-HH. This individual has the general form of the Frisco specimen, but its glabellar ornament is more effaced. The similarity, however, is so great that there must be some doubt about either its source or the source of OU 7216.

Genus **Reedops** Richter and Richter, 1925

Type species.—*Phacops bronni* Barrande, from the Lower Devonian (lower Braník Limestone) of Bohemia.

Remarks.—In 1967 I published a diagnosis of this genus, and since then there have been several papers that have offered further discussion (Ormiston, 1968; Haas, 1969; Alberti, 1970; Přibyl and Vaněk, 1970; Chlupáč, 1972). Each of these authors has emphasized the absence, or the weakness, of the vincular furrow around the front of the cephalon, and the anterior inflation of the glabella. Both these characters are variable, and they cannot be interpreted in a mechanical way. For example, some species, including *Reedops bronni* itself, contain specimens with glabellae that overhang the anterior border only slightly, in a manner no different from that in many species assigned to *Phacops*, whereas the glabellae of some others, such as *R. cephalotes*, have consistently large overhangs. The strength of the anterior vincular furrow also varies from specimen to specimen in some species, but this is of little significance. What is of importance is the overlap of the cephalic margin by the pygidial margin during enrollment, and this may take place either without an anterior vincular furrow or with an obvious one. If there is overlap, the last several pygidial pleural tips have to be modified so that they can cut across the edge of the cephalon. This is accomplished by truncating these tips so that successive pleural ends become progressively more quadrangular. This phenomenon has been observed in several species of *Reedops* (for *R. bronni* see pl. 19, fig. 8), in addition to *R. deckeri* Delo and *R. amsdeni* Ormiston. It also has been noted in *Ananaspis guttulus* (Campbell, 1967, pl. 14, fig. 1). In my experience it is possible to infer from the shape of the vincular furrow alone which method of enrollment an organism adopts, and therefore, as stated previously (Campbell, 1967, p. 33), I regard it as a feature of taxonomic value.

Useful supplementary information on the enrollment method can be obtained from the pygidial margin and doublure. If the margin has to fit into the vincular furrow, it naturally becomes slightly rounded in section and tends to be tucked in. The outer band of the doublure then lies against the narrow floor of the vincular furrow, and therefore it is necessarily narrow, or even sometimes undifferentiated. The inner band of such a doublure is then very steep because it fits against the steep inner edge of the vincular furrow. Such structures are clearly seen in specimens of *Paciphacops* (pl. 8, figs. 1c, 3; pl. 12, fig. 2). On the other hand, if the pygidium overlaps the anterior border of the cephalon, its margin becomes quite sharp, and the outer band of the doublure becomes relatively broad and slightly concave, because it has to fit against the cephalic border. This concave surface continues around to the anterolateral corners of the pygidium, where it forms a distinct notch. The inner band of the doublure is steep and concave. These features are well shown in *R. deckeri* and *R. bronni* (pl. 17, fig. 4a, b).

It must be reiterated that although the vincular furrow and the swollen glabella are of significance in recognizing the genus, they are only two of a large number of distinctive characters, most of which are listed in my diagnosis of 1967. In the light of more recent work, that diagnosis needs minor amendment and supplementation. If we consider only European-African species as representative of the genus—for example, *R. bronni* (Barrande), *R. modestus* (Barrande), *R. cephalotes* (Hawle and Corda), *R. sternbergi* (Hawle and Corda), and *R. maurulus* Alberti—the following features need to be emphasized: The glabellar furrow 1p *does* carry ornament medially in some species, though the furrow can be traced across the medial line (see Alberti, 1970, pl. 15, fig. 8a). The axial furrows on the cephalon and pygidium, and also the pleural and interpleural furrows on the pygidium, tend to be weaker than those of comparable-sized members of the *Ananaspis-Phacops* complex. Even when the eyes are very small, as in *R. bronni,* they lie so far forward and ventrad that there is only a narrow gap between their anteroventral edge and the border furrow. There is always a large postocular platform; i.e., the $\frac{H}{A}$ value is high in comparison with the *Ananaspis-Phacops* complex. The sclera is always depressed below the level of the lenses; and the width of the sclera, except in the uppermost rows of some species, is less than the length of a lens radius. This is in contrast with many species of *Paciphacops* and *Phacops* in which the sclera is high and wide (e.g., *P. rana*). The lenses have intralensar bowls, and several species have diaphragms of some sort (Clarkson, 1969). The fineness and uniformity of the ornament of the whole dorsal surface of the exoskeleton (except where the surface is smooth) is remarkable. On almost all species in the *Ananaspis-Phacops* complex, the ornament varies markedly on different parts of the cephalon, and rarely is the ornament on the axis of the thorax and pygidium comparable with that on the glabella.

Finally, a good hypostome of *R. sternbergi* from Hostim, Bohemia (Palaeontological Museum, Oslo, Number A15581, see pl. 17, fig. 1a, b) has provided much new information and confirms many previously held views. The hypostomal suture is convex backward. The outline of the hypostome is elongate. Its median body is strongly convex in posterior view but much less convex in lateral view. The median furrow is slight, but the strong posterior furrow isolates a long posterior border on which there is a distinct supplementary furrow. The posterior outline is strongly triangular, with a strong median projection flanked on each side by a blunt angle. The anterior wings are of comparable shape to those of *Phacops,* but they apparently lack the peculiar distal pit observed on *P. rana* (Campbell, 1967, pl. 15, fig. 10) and *P. claviger* (Haas, 1969, pl. 82, fig. 5a-c). The posterior wings are situated well back, and in lateral profile the border rises sharply from them toward the rear. The maculae are large and lie in the vertical plane through the deepest part of the posterior wings. The median body and the posterior border are ornamented with slightly elongated pustules arranged with their axes more or less parallel with the contours of the surface. The anterolateral corners of the median body and the inner parts of the anterior wings have much finer granules that are also slightly elongated. Similar granules run in rows down the narrow lateral borders.

Using this information in conjunction with the figures given by Barrande, it is concluded that *Reedops* is characterized by the shape of the hypostomal suture, the posterior position of the posterior wings and the maculae, the supplementary furrow on the posterior border, the median projection on the posterior border, and the nonlinear nature of the ornament on the median body.

There is little doubt that *Reedops*, n. sp., of Haas (1969), *R. deckeri* Delo, and *R. amsdeni* Ormiston form a natural group (see discussion under species). Varying views of the relationships of these species have been expressed. Delo (1940, p. 24-25) thought that *R. deckeri*, although not entirely characteristic of the genus, was closer to it than any other described to that date. Ormiston (1968, p. 1193) placed *deckeri* in *Phacops* because of the structure of the vincular furrow but assigned *amsdeni* to *Reedops* with the clear indication that it was to be compared mainly with the Bohemian species of the genus. Haas (1969, p. 650) was also prepared to accept an assignment of his new species and *amsdeni* to *Reedops*, but he cautioned that as *Reedops* formed "a very inconsistent group of species" and the vincular furrow may have been lost several times within the *Phacops* lineage, the genus *Reedops* was possibly polyphyletic. Alberti (1970, p. 103) compared his *R. maurulus* with *R. amsdeni* and left both in *Reedops*. Chlupáč (1972, p. 400), adopting a totally different view of the relationships, commented that *deckeri* was similar to his species *P. (Phacops?) veles* and was "one of the connecting links between *Ananaspis* Campbell and *Phacops (Phacops)* Emmrich."

As indicated above, the vincular furrow cannot be used to distinguish this group from *Reedops*. The uniform cover of the ornament is similar to that of such species as *R. modestus* and *R. sternbergi*, and the eyes are in a similar position and are little different in lens formula and scleral pattern from these same species. The axial furrows and the pleural and interpleural furrows on the pygidium are rather deeper than is normal for the genus, but they are still comparable to those of *R. modestus*. The hypostome of *R. deckeri* is elongate, has posteriorly placed posterior wings and maculae, and has a supplementary furrow on the rather long posterior border, thus resembling other species of *Reedops*. However, it lacks a median posterior-border projection, and this may be considered significant. It should be pointed out that in the *Phacops* lineage a projection in this position develops late in the sequence, and *deckeri* would be one of the earliest members of the *Reedops* lineage. Further, despite the absence of this projection, the hypostome of *R. deckeri* is much closer to those of *Reedops* than it is to contemporaneous species of the *Phacops* lineage such as *P. logani, P. birdsongensis,* or *P. raymondi.*

I cannot accept the suggestion of Chlupáč that *R. deckeri* is comparable with *P. veles*. The pustules on the glabella of the latter species are apparently in two orders, the larger ones having finer ones scattered between. There are also differences in ornament between the cephalic borders and the cheeks, and the pygidial borders and the pleurae. The vincular furrow is of normal *Phacops* type.

At the present state of knowledge, therefore, it seems to be impossible to distinguish consistently between the *deckeri-amsdeni* group and the European-African species of *Reedops*. Further, I have found no evidence to suggest that the group is polyphyletic. The onus is on advocates of this view to demonstrate a case for consideration.

The parent stock of *Reedops* remains an enigma. I suggested in 1967 that it was a member of the *"Phacops" logani* group, and that the genus originated in the Siegenian. Přibyl and Vaněk (1970, fig. 1) also showed it originating in the late Siegenian, though in the same paper they list certain species as occurring in the Lochkovian of Bohemia. Alberti (1970, fig. 17) indicated a Late Silurian origin. As far as I can determine, *R. deckeri* is the oldest known species, and it is Gedinnian; elsewhere in the world the oldest species are early Siegenian. Therefore, Alberti's suggestion of a Late Silurian origin is probably correct. He indicated *Ananaspis* as the ancestor, and this conclusion has merit for the reason that *Ananaspis* has the same type of enrollment as *Reedops*. Moreover, it is the only comparable genus in a suitable stratigraphic position. Clarkson (1969, p. 202), however, raised an objection to this view, because *Ananaspis communis* has nucleate lenses whereas *Reedops* retains the more primitive intra-lensar bowls. The situation is further complicated by the presence of primitive intralensar bowls in members of the *P. logani* group that are also thought to be descendants of *Ananaspis*. There seem to be three possibilities: (1) the nucleate lens type could have evolved in an isolated stock of *Ananaspis,* while the intralensar bowls remained characteristic of the stock that gave rise to *Reedops* and the *P. logani* group; (2) the nucleate lens type is an artifact of preservation; (3) the origin of *Reedops* and *P. logani* is to be sought in a more primitive genus than *Ananaspis*. It seems to me to be impossible to decide between these possibilities until more information on lenses is available. The matter is discussed further on page 41.

Reedops deckeri Delo, 1935

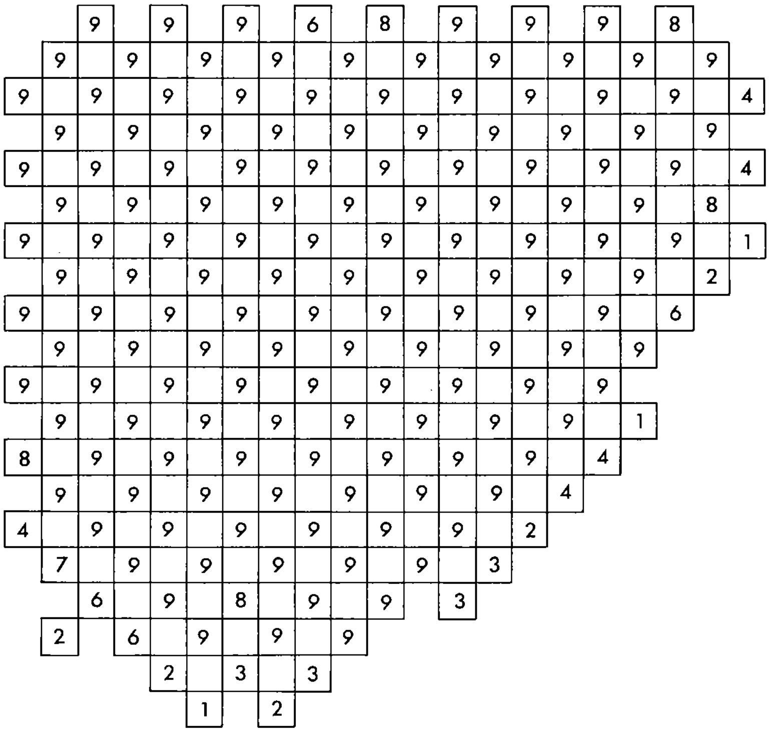
Pl. 6, fig. 4; pl. 16, figs. 1-6; pl. 17, figs. 2-7

Reedops deckeri Delo, 1935, p. 421-2, pl. 48, fig. 1.
Reedops deckeri Delo, 1940, p. 25, pl. 1, figs. 26-28.
Phacops deckeri Delo; Ormiston, 1968, p. 1193-4, pl. 157, figs. 6, 7.

Diagnosis.—Anterior of glabella extends slightly forward of the anterior border; anterior border furrow is present but weak; furrow 1p is represented by a faint, ornamented depression, or absent; furrows 2p and 3p are always clearly visible medially; eyes extend back as far as a transverse line through the median part of furrow 1p and are made up of 140-166 lenses arranged in 20-21 files; vincular furrow is present, but it is vague medially and is narrow and unnotched to faintly notched laterally; hypostomal suture lies almost completely transverse medially; hypostome is elongate, with a pair of small spines at the posterolateral corners and a flightly embayed posterior margin; pygidium has 9 clear rings plus a terminus that is probably composite, and 6 clear pleurae; pygidial doublure has inflected inner edge and narrow posterior embayment; surface of whole exoskeleton, excluding furrows, is covered with rather even, fine tuberculation.

Description.—Cephalon has axial furrows that diverge at 50°-55° in front of 1p, are faintly flexed inward near the front of the palpebral lobe, then drop to make a subangular junction with the border furrow; in lateral profile, occipital ring and glabella near lobes 3p are at about the same level, and lobe 1p is slightly below; in anterior profile sides of glabella are almost vertical, and top is well rounded; occipital ring has poorly defined lateral nodes; in lateral profile, occipital ring is slightly arched on top and drops steeply into the short, deep occipital furrow; occipital ring measures 0.14-0.16 times the glabellar length (sag.); lobe 1p has completely isolated lateral nodes; medial part of furrow 1p fades toward the axial line, where, though it commonly lies in a shallow depression, it is always interrupted by normal glabellar ornament; furrow 2p is normal; 3p has inner part moderately convex forward and isolated lateral part straight, short, and running into the axial furrow opposite the anterior extremity of the eye; palpebral area is gently convex, much lower than adjacent parts of lobe 3p; palpebral furrow is narrow, curved so as to meet the axial furrow at about 80°; palpebral lobe has only a slight outer rim; posterior border furrow is of uniform length (exsag.), almost straight in plan view, and with steep uniform slopes front and back; lateral border furrow swings slightly ventrally after meeting the postocular furrow and then continues around into a weak anterior border furrow; base of eye is not marked by a ridge but merely by a change in slope; rear and front parts of eye drop into postocular and anterior furrows, respectively, but below files 8 to 16 is a distinctive vertical crescentic area with fine ornament. Visual surface of eye has the following characteristics: $\frac{A}{G}$ = 0.40-0.45; $\frac{H}{A}$ = 0.43-0.50; pattern of lenses is as shown on text-figure 18; distance around top of visual surface measures about two-thirds of that around the base; consequently, lenses at top of file are smaller than those at bottom, except in the anterior 4 or 5 files, in which they tend to be of uniform size throughout; largest lenses often are in the most anterior or most posterior file, and they reach a maximum diameter of 0.45 mm in an eye of total length of 6.0 mm; lenses are raised well above the level of the sclera; sclera forms hexagons with slight prominences at the angles and tends to be thicker and more prominent toward the top of the eye.

Glabellar ornament consists of fine tubercles, coarsest posteriorly, and gradually decreasing to little more than half these dimensions anteriorly; on the rear of the glabella about 8-12 per square mm and on the front 20-45 per square mm; on the occipital ring the tubercles diminish slightly in size toward the rear; tubercles on the cheeks inside the border furrow and on palpebral lobes are like those on the posterior part of



Text-figure 18. Statistical pattern of lenses in nine specimens of *Reedops deckeri* from several localities in Haragan Formation. See explanation of text-figure 11.

the glabella; rim of palpebral lobe has fine granules; lateral border has much finer tubercles than adjacent parts of cheeks.

Median length of doublure measures 0.30-0.35 times glabellar length; vincular furrow is narrow, unnotched (almost imperceptible notches on some individuals), and fades abruptly below file 8 of the eye; anterior part of furrow is faint but always distinguishable and always carries the normal doublure ornament; hypostomal suture is almost straight medially.

Hypostome is 10 mm long on a specimen with glabella length of 17 mm, highly vaulted in the posterior view, subtriangular in plan view, but has the posterior extremity truncated; in lateral view, border is straight and almost horizontal between anterior and posterior wings, then straight and downswept to the posterior extremity; there is no anterior border; lateral border begins just behind the anterior margin and is narrow and rather sharp crested as far back as the posterior wings; border behind the posterior wings is only a little wider but distinctly flatter; posterior margin is faintly embayed medially and has a pair of tiny spines in the posterolateral corners; middle furrow is faint (much stronger on internal molds) and is situated in the anterolateral corner of the middle body; macula is prominent and is situated on the flank of the middle body just in front of the line of the posterior wings; supplementary furrow is broad and shallow, branches off from lateral furrow near macula and runs posteromedially to isolate a narrow, crescentic part of the middle body; anterior wing measures about one-quarter the maximum width of the middle body; posterior wing is small; posterior doublure is narrow and has a rounded outline to its inner edge; ventral surface is more or less covered with granules similar in size to those of the cephalic doublure; granules on anterior wings are finer and more densely packed.

Thorax has 11 segments; articulating half ring is approximately equal in length to ring; pronounced lateral nodes are almost completely isolated by deep notches on the front of the ring and much shallower ones on the rear; articulatory furrow is shallow and symmetrical in lateral profile; posterior band of pleurae is higher than the anterior; posterior articulating flange is strong and lanceolate in outline; pleural furrow has an inclined posterior wall and an almost vertical anterior one; furrow is extended onto pleural facet, where it is deflected forward; posterior edge of downturned part of anterior pleura is strongly arcuate, and distal tip is well rounded; on subsequent segments, posterior edge is progressively straighter, and distal extremity is more strongly truncated; length (exsag.) of pleural facet is greatest on anterior segment, diminishing progressively on later segments; medial part of rings and lateral nodes are covered with fine tubercles like those on posterior part of glabella; crest of posterior pleural band and pleural tip behind the facet have similar ornament; anterior band tends to be smooth or has one row of tubercles toward the axial furrow, but distally it has tubercles a little finer than those on the posterior band.

In posterior profile, pygidium is rather flat overall but has a moderately arched axis and a broadly sinuate posterior margin; in lateral profile, crest of axis is gently and evenly curved and passes onto the posterior border with only a minor break; axial furrow is broad and distinctly impressed but fades away almost completely at the posterior extremity of the axis, where it carries normal ornament; axis has 9 clear rings and terminus, which, on well-preserved specimens, has a transverse arrangement of tubercles suggesting that it is composed of 2 or 3 rings; anterior ring has weak lateral notches that are much smaller than those on the posterior thoracic segment and is not separated from the axis by furrows; anterior ring is short because of large articulating half ring and large posterior embayment that is almost half the ring width; next 4 rings have progressively narrower and shorter posterior embayments; in lateral profile, 2d to 5th axial rings tend to be deflected backward approaching the axial furrows, but subsequent ones are straight; 6 clear pleurae are always present, and a faint 7th is present on well preserved-individuals; 1st 4 pleural furrows have long (exsag.), sloping posterior walls, and much shorter (exsag.), almost vertical anterior walls; more posterior furrows tend to become symmetrical; interpleural furrows are slight but distinct; both pleural and interpleural furrows fade laterally, to leave a broad unfurrowed border; no border furrow is present. Margin of pygidium is sharp; doublure is divided into 3 bands, an outer, slightly concave band, separated from a slightly wider middle band by a marked ridge that is continued in across the anterolateral corners toward the fulcrum, and a rimlike inner flange that is of uniform width except at the posterior extremity, where it is embayed so that its edge lies directly beneath the terminal part of the axial furrow; whole doublure is covered by fine granules.

Remarks.—*R. deckeri,* as pointed out by Ormiston (1968, p. 1193), has coarser glabellar ornament than *R. amsdeni,* which is its nearest relative. The ornament on one or two specimens of *R. deckeri* from Old Hunton Townsite is finer than normal, but it never approaches the dimensions of *R. amsdeni.* Ormiston's other points of difference, including the continuity of the vincular furrow, the junction between the 1p furrows, and the length and depth of the 2p furrows, are not of much consequence. As shown above, the vincular furrow of *R. deckeri,* though continuous, is always weak, and furrow 1p is interrupted by ornament medially. As shown on plate 16, figures 1b, 2, 6, the furrows 2p are little different from those of *R. amsdeni.* Ormiston's comments were based mainly on the holotype of *R. deckeri,* a specimen that was badly prepared, and except for cephalic ornament, the most important feature separating these two species is the greater number of lenses in the eye of *R. amsdeni.*

Ormiston's view that *R. amsdeni* is a morphological (and possibly an evolutionary) intermediate between *R. bronni* (Barrande) and *R. modestus* (Barrande) is not supported by the present study. *Reedops* seems to have evolved from a highly and uniformly ornamented form with rather large eyes, and hence the partly smooth *bronni,* with its relatively small eyes, is on a morphologically advanced side-branch of the main evolutionary plexus. The younger *modestus* is more probably a descendant of a species like *R. sternbergi* (Hawle and Corda). Moreover, in details such as the strength and position of the palpebral furrow and palpebral lobe, the number of lenses and number of files in the eyes, the subocular crescentic strip, and the number and strength of the axial, pleural, and interpleural furrows in the pygidium, *R. amsdeni* is closer to *R. deckeri* than it is to either *R. bronni* or *R. modestus.*

Reedops, n. sp., of Haas (1969) has a vincular furrow that is notched laterally, many fewer lenses in the eye, and a finer glabellar ornament than *R. deckeri.*

R. maurulus Alberti from the Pragian of Morocco, which Alberti (1970, p. 103) compared to *R. amsdeni,* also has features in common with *R. deckeri,* but its eye is smaller and its cephalic ornament is finer.

Material.—(Not all specimens available are listed.) OU 6556, Haragan Formation at Vines Dome, NW¼NW¼ sec. 2, T. 2 S., R. 2 E., Murray County; OU 3276, OU 5376-78, OU 6557, OU 6559, USNM 183890 (several specimens), all from the vicinity of Old Hunton Townsite, NW¼ sec. 8, T. 1 S., R. 8 E., Coal County; OU 6558, OU 6560, OU 6561-63, USNM 187025 from the vicinity of White Mound, NE¼ sec. 20, T. 2 S., R. 3 E., Murray County.

Superfamily DALMANITACEA Vogdes, 1890

Remarks.—Of the several families placed in this taxon by Richter and Richter and Struve (*in* Moore, 1959), only the Dalmanitidae is specifically dealt with in this bulletin, and with this family only the Dalmanitinae and Synphoriinae require comment. The Synphoriinae was discussed recently by Lespérance and Bourque (1971) and by Lespérance (1975), the latter suggesting that it should be raised to family rank to incorporate two subfamilies, the Synphoriinae and the Trypaulitinae. These authors espoused and expanded the proposal of Delo (1935, 1940) that the main diagnostic feature of the synphoriinids is the coalescence of glabellar lobes 2p and 3p. All grades of coalescence are found, and to give precision to the concept, Lespérance proposed that it be considered present only when furrow 2p does not join the dorsal furrow *on the external surface*. However, even this criterion is difficult to apply because of variability in the sharpness of incision of furrow 2p, as can be seen by reference to his plates.

In trying to determine the relationships of the forms described herein, particularly those assigned to *Huntonia (Huntonia), Huntonia (Neoprobolium), Huntonia (Prosocephalus), Phalangocephalus*, and *Odontochile*, I have had considerable difficulty, and I have been led to a reexamination of these subfamilies and the criteria on which they are based.

If we consider all the genera assigned to the Dalmanitinae and the Synphoriinae the following morphological points seem to me to be of importance.

1. *Cephalic apodemes.* There are three basic patterns in the arrangement of the apodemes on the cephalon. They are not all known in equal detail.

a. The dalmanitinid pattern, described below under "Aspects of functional morphology," has the gap between 1p and 2p less than 1.5 times the gap between the occipital and 1p apodemes; 1p is transverse and almost at right angles to the sagittal line in dorsal view, and 2p is transverse or has a slight posterior deflection at its inner end. This is characteristic of *Dalmanites* and *Odontochile*.

b. The synphoriinid pattern has the gap between 1p and 2p more than 1.5 times the gap between the occipital and 1p apodemes. 1p is still transverse but is inclined to be slightly oblique to the sagittal line. 2p tends to be equidimensional in dorsal view. It is this shape of apodeme 2p that produces the short furrow 2p emphasized by Delo and by Lespérance. It is not certainly known if the occipital and 1p apodemes of this type have the dalmanitinid form, but judging from the figures of *Synphoria pricei* given by Lespérance (1975, pl. 1, figs. 2, 8), they do not. This pattern is characteristic of *Synphoria* and *Anchiopsis*.

c. The trypaulitinid pattern has the occipital, 1p, and 2p apodemes spaced as in the synphoriinid pattern, but 1p is a slender structure with its axial end curved strongly forward in dorsal view. Apodeme 2p is almost completely equidimensional in dorsal view and lies close to the axial extremity of 3p. The forward curve of 1p and the position and shape of 2p produce distinctive "longitudinal" furrows. These features are well illustrated for *Trypaulites* by Lespérance (1975, pl. 3, figs. 6, 7, 10). The shapes of the various apodemes toward their ventral ends are quite unknown.

This analysis is more meaningful than one in terms of the glabellar furrows because it is indicative of different modes of attachment of the various muscles to the exoskeleton, and this in turn is indicative of different enrollment styles.

2. *Borders, doublures.*

a. Members of the dalmanitinid group characteristically have a well-defined broad cephalic border on which is a shallow epi-border furrow. This type of border is always associated with a doublure that has a flat outer portion and a steeply upturned inner portion. *Dalmanites* and *Odontochile* are characteristic.

b. Other genera, such as *Synphoria* and *Anchiopsis,* have a narrow, convex, poorly defined border. The lateral parts of the doublure are correspondingly narrow and are rather evenly rolled, or have a slight vincular furrow.

Naturally, these two types of cephala have corresponding pygidia, that is, with well-defined borders and flat doublures, or with weak to absent borders and narrow rounded doublures.

c. The cephalic border of *Trypaulites* is well defined and broad, but it has no clearly defined epi-border furrow. The nature of the doublure remains unknown to me. The pygidium also has a clearly defined border, but the doublure is surprisingly narrow and is rolled rather than flat (see Lespérance, 1975, pl. 3, fig. 2, left side; by courtesy of Dr. Lespérance I have seen a plaster cast of this specimen).

3. *Genal spines.* There is also a correlation between the cephalic border form and the shape of the genal spines. Genera with a wide, well-differentiated border tend to have longer genal spines than those with narrow borders. The long-spined types fall into two categories:

a. The dalmanitinid type has rather bladelike spines that apear to be hollow-ground on the outer face owing to the extension of the epi-border furrow down its length (see Campbell, 1967, pl. 17, fig. 7). Note that the lateral border furrow stops in front of the base of the genal spine below the end of the lanceolate posterior border furrow.

b. The trypaulitinid type of spine has a similar shape, but it is the lateral border furrow, not the epi-border furrow, that is extended down its length. Note that in this group also the posterior border furrow does not join with the lateral border furrow.

The synphoriinid type, on the other hand, does not always have genal spines. If they are present, they are short and do not have the lateral border furrow or the epi-border furrow extending along them. Consequently, the spines tend to be ovate in section. There is probably a junction between the posterior and the weak lateral border furrows at the base of the genal spine, but I have been unable to confirm this (but see Lespérance and Bourque, 1971, pl. 27, fig. 6).

4. *Thoracic architecture.* There are three types of thoracic segment, recognized mainly by the pleural morphology:

a. In the dalmanitinid type the pleural furrow dominates the pleural region and turns back to form a lanceolate terminus on the crest *behind* the broadly downturned facet. The distal tip of this facet is pointed and on the more posterior segments is commonly extended into a bladelike spine. On the first segment the facet sits beneath the posterior border of the cephalon and undergoes very little movement during enrollment. In this type, the posterior pleural band is weak and slopes gently forward into the pleural furrow; the anterior band is stronger and drops steeply back into the pleural furrow.

b. In the synphoriinid type the posterior pleural band is thick and well rounded, and the anterior band is thin. The pleural furrow is not dominating, but rather is gash-like, and distally it runs either ventrally or anteroventrally to the facet. This facet is broad and has a well-rounded ventral edge similar to that of the Phacopinae. It never terminates in a spine. The Panderian notch is quite phacopoid. It is well illustrated by *Synphoria* (Lespérance and Bourque, 1971, pl. 27, figs. 5, 8) and by *Odontocephalus* (Hall and Clarke, 1888, pl. 11B, figs. 3, 4). It is difficult to appreciate the relationship of the first segment to the cephalon in this type without seeing the material, but the enrolled specimen of *Odontocephalus selenurus* figured by Hall and Clarke (1888, pl. 12, figs. 10, 11) suggests that enrollment was spheroidal like *Phacops,* rather than dalmanitinid. This implies considerable movement on the first thoracic segment and hence some special modification of the genal region of the cephalon. It is a matter requiring further investigation.

c. The trypaulitinid type is not well known. *Trypaulites* itself (see Stumm, 1954, pl. 3, fig. 1; Lespérance, 1975, pl. 3, figs. 2, 3) has the same structure of pleural bands and pleural furrows as *Synphoria*, but the pleural tips are not curved forward in a broad arc as they are in that genus. As far as

I can determine, the tips are more or less truncated on the more anterior segments but become produced into slight, obtuse spines on the more posterior segments. The nature of the enrollment and the Panderian notches remains unknown.

5. *Pygidial architecture*. Corresponding with the above thorax types there are three types of pygidium. Since the pygidial segments are serially modified forms of the thoracic segments, these also are recognized mainly by the structure of the pleurae; the number of segments is largely irrelevant. Naturally, the distinctive characters will be best exhibited by the first few segments.

a. The dalmanitinid type exhibits the dominant lanceolate pleural furrow, the weak posterior band that tends to fade away toward the border, and the strong anterior band that drops steeply into the pleural furrow (Whittington and Campbell, 1967, pl. 14, fig. 12). This is the "asymmetric pygidial rib" of Lespérance (1975), which he has described using "rib" rather than "pleural" terminology. The facet on this type is always rather narrow, bounded all the way round its posterior edge by the anterior band of the pleura, and behind that again by the pleural furrow. It invariably has an obtuse process to lock into the Panderian notch of the last thoracic segment (pl. 22, figs. 4a, 5a; Campbell, 1967, pl. 16, fig. 10).

b. On the first few segments of the synphoriinid type, both the anterior and posterior bands are well developed, and the posterior band does not fade toward the border. The pleural furrow is not deflected backward distally (though on the more posterior segments it commonly is). On the first segment it tends to run down onto the edge of the pleural facet (see Lespérance, 1975, pl. 2, fig. 3). Little is known of this region of *Synphoria* and its allies, and the nature of the locking device on the facet has not been described or illustrated.

c. The trypaulitinid type is characterized by posterior bands that are somewhat smaller than the anterior bands and by pleural furrows that are of uniform dimensions from axis to border. The posterior band does not fade toward the border as it does in the dalmanitinid type, and though the anterior slope of the pleural furrow is steeper than the posterior slope, the "asymmetric" rib structure of the dalmanitinid type is not reached. On the other hand, the pleural furrow is a much more dominant structure than in the synphoriinid type. The facet on the first segment is more dalmanitinid than synphoriinid, as might be expected from the shape of the pleural tips on the posterior thoracic segments (see Lespérance, 1975, pl. 3, fig. 8, 8a).

6. *Pygidial apodemes*. All members of the *Dalmanites-Odontochile* group have transverse pygidial apodemes that are concave on their anterior face (see discussion below). *Synphoria* and *Anchiopsis*, on the other hand, have very concentrated apodemes (see Lespérance and Bourque, 1971, pl. 26, figs. 6, 7, 9; pl. 27, figs. 2, 5) that are equidimensional in cross section and spikelike in form. They are also more discrete than those of *Dalmanites*, in that there is almost no connection between the apodeme proper and the axial furrows. It should be noted that in assessing this character it is necessary to examine the internal surface. The exoskeleton is so thick that a misleading impression of the apodemal shape is obtained from the external surface. The apodemes of the trypaulitinid group are unknown.

The most important points to come out of the above discussion are as follows:

1. There are three basic types of general structure within the genera previously assigned to the Dalmanitinae and Synphoriinae. Two of these, the synphoriinid and the trypaulitinid, correspond with the divisions of the Synphoriidae proposed by Lespérance (1975), but the composition of the groups is not the same as he suggested.

It seems to me to be difficult, if not impossible, to transform the dalmanitinid into the synphoriinid morphology, or *vice versa*. Further, the differences are so clear cut and are spread through such a variety of genera that they must represent well stabilized and strongly adapted patterns. On the other hand, the synphoriinid and trypaulitinid patterns have a great deal in common, and they could be derived from a common stock. They must have become separated in the Late Silurian or Gedinnian (for stratigraphy, see Lespérance, 1975, fig. 3). The recognition of a family Synphoriidae by Lespérance to include the Synphoriinae and Trypaulitinae has much to commend it.

2. *Roncellia* and *Forillonaria* (at least as represented by their type species) are both

basically dalmanitinid in structure. None of the above points provides a reason to consider them related to the Synphoriidae. It is true that *Roncellia* has a modified anterior cephalic border like that of certain species of *Synphoria,* but for reasons given below this is not considered to be indicative of relationships. In fact, I find it difficult to consider *Roncellia* any more than a subgenus of *Odontochile*, and *Forillonaria* is probably a synonym of *Odontochile*.

This raises the problem of the origin of the synphoriinids again, a problem to which there is no definite answer at present. The oldest synphoriinid (*Synphoroides vetustus* Lespérance, 1975) is of Gedinnian age, and hence the parent stock will be Gedinnian or older. It is possible that some Silurian species such as the one described as *Dalmanites (Synphoria) arkansanus* by Van Ingen (1901) was close to this parent stock. It has an appropriately shaped glabella, and synphoriinid (in the sense of the above discussion) cephalic apodemes, borders, doublures, genal spines, pygidial pleurae, and pygidial facets. The apodemes 2p are not equidimensional as in *Synphoria*, but the apodeme spacing is correct. The number of pygidial axial rings is low in comparison with the figure suggested by Lespérance (1975) for the ancestral stock, but this estimate was based on a generalization about the evolutionary reduction of pygidial segmentation. That this cannot be applied indiscriminately to the dalmanitaceans is shown by the evidence that *Odontochile* developed from *Dalmanites* by an *increase* in pygidial segmentation. Of course, there is a time gap between the known occurrences of the *arkansanus* group (Wenlockian) and the earliest symphoriinids, but given the present state of knowledge of American Late Silurian trilobites, this can scarcely be regarded as a strong argument.

3. *Neoprobolium*, as interpreted from its type species, is entirely dalmanitinid in structure, and Lespérance and Bourque (1971) were obviously correct in excluding it from the Synphoriinae.

4. *Phalangocephalus* (new genus) is undoubtedly dalmanitinid. Although at first sight the cephalic border seems to be too narrow and the cephalic doublure too tightly rolled to belong to this type, the interpretation of the marginal spines as the product of indentation of the outer part of the border permits their recognition as dalmanitinid. Any residual doubt is removed by the form of the genal spines and the pygidial architecture. There is no possibility that its marginal cephalic spines are indicative of a relationship with *Odontocephalus*.

5. *Odontocephalus* is typically synphoriinid in its thoracic and pygidial characteristics (including the overall shape, pleurae, border, and doublure) and in its cephalic posterior border furrow and genal region. On the other hand, the lateral cephalic border and genal spines are more reminiscent of the trypaulitinid type, and the tendency to develop longitudinal glabellar furrows is also suggestive of the same type. These points merit further discussion. The cephalic apodeme 2p is often placed close to the axial end of 3p, but as is well shown by the figure of Eldredge (1971, pl. 14, fig. 9), apodeme 1p is a massive structure unlike the delicate structure in *Trypaulites*. In fact, these two apodemes are so massive that they distort the dorsal exoskeleton into longitudinal furrows. The similarity of *Odontocephalus* to *Trypaulites* in this respect is therefore of little significance. On the other hand, the cephalic border and the genal spines do not seem to be distinguishable from those of *Trypaulites*. (I have not been able to examine these structures at first hand, but the published photographs given by Stumm [1954, pl. 2, figs. 5-7] and the figures given by Hall and Clarke [1888, pl. 11B, figs. 1-4] leave little room for doubt.) The doublure of *Odontocephalus* seems to be well rounded laterally, like that of *Synphoria*, but it may also resemble that of *Trypaulites*, which is not known in detail. This suggests either that borders and genal spines have been developed independently in the *Synphoria* and *Trypaulites* groups or that *Odontocephalus* is on a side branch leading from the *Synphoria* to the *Trypaulites* group. The latter does not seem likely from what is known of the stratigraphy of these genera.

6. The position of *Coronura* is in my view not completely clear, mainly because certain significant details are not yet available. The cephalic apodemes (see Stumm, 1954, pl. 1, fig. 1), and probably the cephalic border, are of trypaulitinid type. The architecture of the pygidial pleurae and probably the thoracic pleurae are also trypaulitinid. Almost noth-

ing is known of the doublures, though the above mentioned figure of *C. aspectans* shows that it is very wide on the pygidium. If *Schoharia* is accepted as a close relative of *Coronura*, as Lespérance has suggested, this supports the idea that a wide doublure is characteristic (Lespérance, 1975, pl. 6, fig. 5). The weight of evidence certainly favors the closer relationship of *Coronura* with *Trypaulites* than with *Synphoria* and its allies. This is not opposed by the evidence of the number of thoracic segments, of which they all have 11. The report of 12 in *Trypaulites* is not correct (see Lespérance and Bourque, 1971, 1973).

7. Anterior modification of the cephalic border has taken place entirely independently in different dalmanitacean stocks. The radial spines of *Phalangocephalus* and *Odontocephalus* are excellent examples of homeomorphy. It seems likely that many of these modifications, whether they involve single or multiple projections, are adaptations enabling the animal to take in and expel water (presumably to maintain an appreciable respiratory level), while at the same time remaining tightly enrolled (presumably for protection). This matter is discussed further under "Aspects of functional morphology."

TABLE 2.—MORPHOLOGICAL COMPARISON OF THE DALMANITINAE, SYNPHORIINAE, AND TRYPAULITINAE

D, dalmanitinid; *S*, synphoriinid; *T*, trypaulitinid

	Cephalic apodemes			Borders doublures			Genal spines			Thoracic architecture			Pygidial architecture			Pygidial apodemes	
	D	S	T	D	S	T	D	S	T	D	S	T	D	S	T	D	S
Dalmanites	X			X			X			X			X			X	
Odontochile	X			X			X			X			X			X	
Neoprobolium	X			X			X			X			X			X	
Roncellia	X			X			X			X			X			X	
Forillonaria	X			X			X			X			X			X	
Huntonia	X			X			X			X			X			X	
Phalangocephalus	X			X			X			X			X			X	
Synphoria		X			X			X			X			X			X
Synphoroides		X			X			X			X			X			X
Anchiopsis		X			X			X			X			X			X
Odontocephalus		X			X			X			X			X			X
Trypaulites			X			X			X			X			X	?	
Coronura			X			?			X			X			X	?	
Schoharia	Unknown			Unknown			Unknown			Unknown					X	?	
Corycephalus		?		Unknown					?	Unknown			Unknown			Unknown	

Family DALMANITIDAE Vogdes, 1890

Remarks.—Having excluded the synporiinids from this family, we are still left with a wide variety of subfamilies according to the classification adopted in Moore (1959). Understanding of many of these subfamilies is still being developed. For example, I have attempted to show elsewhere that the Zeliszkellinae, as defined in the Treatise on Invertebrate Paleontology, is a polyphyletic group (Campbell, 1973); and the composition and relations of the Asteropyginae are in need of a revision which is beyond the scope of this bulletin. Accordingly, no attempt is made herein to list the diagnostic characters of the family or to indicate the subfamilies assigned.

Subfamily DALMANITINAE Vogdes, 1890

Remarks.—Relationships between the species in this family are poorly understood, and the generic groupings that have been suggested for these species are anything but satisfactory. In order to assign the various Oklahoma species described in this bulletin, the definitions and relationships of the following established genera and subgenera (not all of them valid) have had to be clarified:

Dalmanites Barrande, 1852
Odontochile (Odontochile) Hawle and Corda, 1847
Odontochile (Zlichovaspis) Přibyl and Vaněk, 1970
Odontochile (Kazachstania) Maksimova, 1972
Odontochile (Reussia) Maksimova, 1972
Neoprobolium Struve, 1958
Roncellia Lespérance and Bourque, 1971
Forillonaria Lespérance, 1975
Corycephalus Hall and Clarke, 1888

1. *Odontochile* is said to differ from *Dalmanites* mainly in its larger size, its more strongly segmented pygidium, its more denticulate hypostomal border, in having facial sutures lying outside the anterior furrow, and in its wider doublures (see Richter, Richter and Struve *in* Moore, 1959, p. O472). The distinction between the two genera in North America has never been clear, as was pointed out by Delo (1940, p. 55), and emphasized again by Maksimova (1972, p. 92). In my view, the two genera intergrade, and the boundary will remain indefinite, for the reason that not all the trends along which evolution was taking place were proceeding at the same rate everywhere. As a result, a species like *D. rutellum* Campbell, which has been placed in *O. (Kasachstania)* by Maksimova, has the size, pygidial segmentation, and doublures of a typical *Dalmanites*, but the anterior limbs of its facial sutures are like those of an *Odontochile*. Its hypostome is unknown. While the definition of the genera is in terms of evolutionary grade in a number of evolving characters, the assignment of such species must remain arbitrary.

2. Přibyl and Vaněk (1970) distinguished *O. (Zlichovaspis)* (type species *O. rugosum* Hawle and Corda) from the nominate subgenus by the greater sharpness of definition of the glabellar furrows and lobes in the middle part of its glabella, the greater length of the ϵ-ω part of the facial suture, the shape of the interpleural furrows, and the presence of a tongue-shaped anterior cephalic process. Without examining the material it is difficult to be certain of all these details, but from my own observations of the variability of the definition of the glabellar furrows, the shapes of the posterior limb of the facial suture, and the interpleural furrows in other dalmanitinids, I find it difficult to accept these characters as being of subgeneric significance. The ventral surface of the anterior process is not described, but the shape of the border and the pygidial doublure suggest that there is no difference between this species and *O. hausmanni* in the way these two structures meet on enrollment.

3. Maksimova's division of *Odontochile* into three subgenera is based almost entirely on the following pygidial characters: (1) proportions of pygidium, (2) shape of axis, (3) shape of anterolateral corners, (4) shape of posterior spine, (5) number of axial rings and pleurae, and (6) width of doublure.

It may be of importance to note that, in the North American dalmanitinid material, characters 1, 2, 4, and 6 are sexually dimorphic, and hence caution should be exercised in applying them in taxonomy at this level. The apparent shape of the anterolateral corners as seen in any given specimen is very considerably affected by the degree of exposure of the articulatory facet. Although this is potentially a valuable character because it reflects the amount and angle of deflection of the thoracic pleural tips and hence the style of enrollment, it is difficult to accept that, for example, *O. (O.) pristina* Maksimova is any different from *O. (Reus-*

sia) batymarginatia Maksimova in this respect (cf. Maksimova, 1968, pl. 25, fig. 2, with pl. 27, fig. 3). The length of the axis is correlated with the width of the doublure, as the doublure always extends in to the end of the axis; the overall proportions of the pygidium are strongly correlated with the number of axial rings and pleurae, and with the shape of the anterolateral corners. Consequently, the extent to which all these characters can be regarded as independent variables in the definition of subgenera needs careful examination.

4. *Neoprobolium* has remained poorly known despite the fact that its type species, *Asaphus nasutus* Conrad, 1841, has been long established and is well preserved. Through the courtesy of Dr. D. W. Fisher and Dr. R. Conrad of the New York State Museum, I have been able to examine casts of the specimens figured by Hall (1861, pl. 75, fig. 2, pl. 76, figs. 1-8) and a small number of specimens from the Hall collection. Some of them are refigured herein (see pl. 18, figs. 1-5;). It is not known how representative these specimens are of the whole population, whether there is any evidence of dimorphism, or even if the heads and tails have been correctly associated. For present purposes the assumption is made that they are adequate to provide a description. This is as follows.

Exoskeleton is large and moderately convex; glabellar furrows show normal dalmanitinid pattern; anterior glabellar lobe is subrhombic in outline, drawn out in front; lobes 3p are laterally elevated above the medial part of the lobe; palpebral furrow is deep and tends to be V-shaped in outline; palpebral rim is steep but has a flattened crest; facial suture lies outside the preglabellar furrow, β is well-rounded, γ lies opposite the anterior end of lobe 3p, and ϵ opposite the anterior end of lobe 1p; eye has about 45 files of 10 or fewer lenses; there is a strong horizontal platform below the eye; free cheek below platform drops steeply to a strong lateral border furrow; lateral border also slopes but at a smaller angle; epi-border furrow is shallow but definite, fading anteriorly, but continues onto the genal spine; width of border diminishes slightly at the base of the anterior process; width of anterior process decreases gradually toward its tip, where it divides to produce 2 slender termini that are curved dorsolaterally; in lateral profile, anterior process is curved broadly upward; posterior border is long (exsag.), and lateral to the fulcrum is curved back in a broad arc to form a strong, broad base for the genal spine; posterior border furrow is lanceolate and stops short of the lateral border furrow; glabella has moderately large tubercles more or less evenly distributed, and finer tubercles (or granules) scattered between them; cheeks, genal spines, and anterior process have closely spaced granules; free cheek below the eye platform has caecal reticulum.

Doublure has a wide, flat outer portion separated by a right-angular flexure from a vertical inner portion which, on the lateral region of the cephalon, is as high as the outer portion is wide; hypostomal suture is slightly concave; ventral surface of anterior process is flattened to slightly concave; surface of doublure (except vertical inner part) has fine granules; hypostome unknown.

Thorax is unknown.

Pygidium has 15 or 16 complete rings, 1 incomplete, and a terminus; 13 pleural furrows visible, the last one almost co-linear with the axial furrow; first pleurae are turned back markedly at their tips, but successive ones become straighter, and the last 3 or 4 are flexed slightly forward at their tips; interpleural furrows are clearly defined on all except the last two pleurae; axis is well defined posteriorly; post-axial ridge is high, well rounded in cross section, and continues into a spine about 1.5 times the length of the axis; proximal part of spine is slightly upturned, although most of it is horizontal; spine is almost circular in cross section; dorsal surface is completely covered with granules like those on the cheeks; there are scattered irregular swellings on both rings and pleurae. Doublure has wide, flat to gently convex outer portion and a very narrow upturned inner portion; posteriorly, doublure does not quite reach the end of the axis and is not deeply embayed; outer portion is granulate.

N. tridens (Hall), although imperfectly known, is commonly placed with *N. nasutum* (Delo, 1940). The long anterior process, long and broadly based genal spines, and glabellar ornament suggest a close relation between these species (Clarke, 1908). The main difference lies in the trifid rather than bifid nature of the tip of the process. The pygidium is unknown.

Unlike Delo (1940, p. 77), I do not accept *Dalmanites palaceus* Savage as a close relative of the above species. It is dealt with below.

Diagnosis of *Neoprobolium*.—These are large, moderately convex dalmanitinids; anterior glabellar lobe is extended forward to produce a subrhombic shape; lateral border is inclined, only slightly constricted at the base of the anterior process; posterior border is arched posterolaterally and increases in length (exsag.) to form a broadly based genal spine; anterior process measures about half as long as the glabella and is curved gently upward toward the tip, where it is divided into 2 or 3 short lobes; ϵ on facial suture is situated well forward of the border furrow and well out from the axial furrow; cephalic doublure has a wide flat outer portion and a high steep inner portion. Pygidium has a wide axis; there are about 16 axial rings and 13 pleural furrows; border is narrow; terminal spine is long and slender; doublure is wide and has a low upturned portion.

5. As has been shown in the discussion of the differences between the synphoriinids and the dalmanitinids, *Roncellia* is characteristically dalmanitinid. It has not been compared with *Odontochile* in previous work. Considering both the type species (*R. debeaujeuensis*) and *R. telosensis* together as representative of the genus (a procedure justified by the fact that they have most cephalic characters in common and they occur in sequence in Gaspé), *Roncellia* may be considered as an *Odontochile* with a slightly modified anterior cephalic border. The report of a distinctive 12 thoracic segments is not correct (Lespérance and Bourque, 1973). The anterior cephalic process apparently does not lock with the pygidial doublure as does that of *Huntonia (Huntonia)*. Only one type of pygidium is figured for *R. debeaujeuensis* (Lespérance and Bourque, 1971, pl. 25, fig. 3), and it has the characteristic form of a Type C morph of such species as *H. (Huntonia) purduei* described below. It would be of interest to know the range of form of the pygidia found in association with this Canadian species.

6. *Forillonaria*, which I interpret in terms of its type species, *F. russelli* Lespérance, is also dalmanitinid rather than synphoriinid. Its anterior cephalic margin has a broad, rounded "process," with the border unmodified at its base. The terminal pygidial spine is reduced to a nub, and in this respect it differs from other species of *O. (Odontochile)*; but it is doubtful if this difference is of generic importance. In Lespérance's view, *Forillonaria* gains significance because it is the root stock of other members of his Trypaulitinae, but as has been shown above, this is still a disputed matter.

7. *Corycephalus* is known only from its type species, *Dalmanites regalis* Hall. In Moore (1959), the pygidium figured as representative of the genus belongs to *Phalangocephalus dentatus,* a species which is only remotely related to *regalis,* although it is said to be congeneric by Delo (1940) following Hall and Clarke (1888).

I have not examined any of the type material. From the figures available, it appears that the genus is characterized by its enormous convexity; blunt, ventrally directed marginal spines; and peculiarly swollen glabella. No pygidium is known. I am not convinced that it belongs within the Dalmanitinae.

A note on pygidial rings and pleurae

A common feature in dalmanitinids is the presence of incomplete axial rings near the posterior extremity (see Whittington and Campbell, 1967, pl. 14, fig. 12). These are counted as rings by some workers but are referred to as the undifferentiated terminus by others. This makes for considerable confusion. Take, for example, *H. (Huntonia) huntonensis* for which Delo (1940, p. 42) recorded 14 rings plus a terminus. His figures seem to show 15 plus a terminus. Examination of the holotype, which is poorly preserved in this region, indicated that 15 is probably correct, but the figured paratype (Delo, 1940, pl. 4, fig. 28) clearly shows 15 complete rings, 1 incomplete ring, and a terminus. Since a difference of 2 or 3 in the ring count is often listed as diagnostic, this discrepancy is a matter of importance. Consequently, all ring counts listed herein are in terms of the number of complete and incomplete rings.

It is customary also to list the number of pleural ribs, often without indicating if the first half rib is included in the count. It is less ambiguous, and a more meaningful reflection of the number of pleurae present, to list the number of pleural furrows. The last furrow is sometimes difficult to see unless the external surface of the posterior pygidial extremity is well preserved. Consequently, I have listed the number observed, and if it appears that there is space for another that could have been destroyed, I have listed it as a possibility—for example, "13 or possibly 14 pleural furrows."

Dimorphism in dalmanitinids

In 1968, I suggested that *Dalmanites rutellum* exhibited dimorphism of the pygidium, but there was insufficient material then to establish a case. The evidence now available from Early Devonian species is much stronger.

Specimens from the following units have been examined: (1) Ross Limestone, Pickwick Dam, western Tennessee; (2) Birdsong Formation, Big Sandy River, western Tennessee; (3) Haragan Formation, Oklahoma; (4) Fittstown Member, Oklahoma.

From none of these is it possible to know the vertical and horizontal limits on the available collections. However, the Fittstown Member collection came mainly from one 2-3-foot bed and is in one lithology (see Amsden, 1960, p. 286, collection P16). It is probably a sample of a single population or a closely related group of populations. Both the Ross and the Birdsong collections also are found in uniform and distinctive lithologies, and there is no reason to believe that they represent mixtures of two or more separate populations. The Haragan material comes from a number of widely separated localities that are of similar, but not identical, ages.

The Haragan contains a variety of dalmanitinids, but the collections from each of the other units have only 2 or 3 types of pygidia and apparently 1 type of cephalon, though the number of cephala is always small. All the non-Haragan pygidia are characterized by having 18-22 axial rings that are flattened laterally, 14-16 pleural furrows, pleurae that are "shingle-like" in lateral profile, and fine, rather uniform granulation overall. The three types of pygidia can be readily distinguished by the characters shown in table 3.

These three types do not occur in equal numbers. For example, of the 8 Pickwick Dam specimens assignable to a type, there are 4 Type A, 2 Type B, and 2 Type C. The other localities also show a greater abundance of Type A, and the Fittstown collection contains no Type B among 11 specimens.

The evidence that 3 groups can be recognized at 2 of the 3 localities suggests trimorphism. Similar triplets can be recognized in the Haragan; they are assigned to the same species as the Pickwick Dam ma-

TABLE 3.—TYPES OF PYGIDIA IN DALMANITINIDS

	Type A	Type B	Type C
Size:	Reaches a larger maximum	Smaller maximum	Intermediate
Outline:	Peltate	Subtriangular	Subtriangular
Terminal spine:	Short, broad-based, depressed; triangular in cross section, subhorizontally projecting	Long, narrow-based; circular in cross section away from base and inclined upward	Long, narrow-based; circular in cross section away from base but directed horizontally
Border:	Wide, tending to be horizontal	Narrow and inclined	Narrow and inclined
Doublure:	Wide and flat laterally, with narrow, upturned inner rim	Narrow, inclined laterally, with a proportionately more marked inner rim	Narrow, gently inclined laterally, with prominent inner rim
Axis:	Bluntly rounded, well-defined terminus; broad, weak, postaxial ridge	More acute terminus, poorly defined, continued into postaxial ridge forming base of spine	Acute terminus, well defined, with weak postaxial ridge joining at lower level

terial, *H. (Huntonia) purduei,* adding further support to this concept. Although it is difficult to obtain information from other units, there is some evidence that the same thing is true of the same species group in the Bailey Limestone of Missouri (Tansey, 1922) and the Coeymans Limestone of NewYork (Hall, 1861; Delo, 1940). Tansey (1922, pl. 44, figs. 5-7) figured pygidia of two types but merely referred them to *Dalmanites* sp. The type of *Odontochile micrurus* (Green), from the Coeymans (Delo, 1940), is another member of this species group, and it is clearly a Type B. I have seen other material from the same formation at Clarksville, New York, that would fall into Type A of the same species.

None of the pygidia I have examined from the above collections has been articulated with both a thorax and a cephalon. The associated cephala are very few in number: 1 almost complete and several fragments from Pickwick Dam; 2 almost complete and 1 fragment from Big Sandy River; 4 fragments from the Fittstown Member; 1 almost complete and 2 fragments from the Haragan. Along with other similarities, all these specimens are characterized by a depressed glabellar profile, a complete cover of microgranulation, and a short, broad, flattened anterior cephalic process. One of the features of these dalmanitinids (see discussion on morphology) is that the anterior cephalic process fits neatly against the posterior part of the pygidial doublure during enrollment. It is clear that although Type A doublures would neatly complement the anterior cephalic processes mentioned above, Type B would not. This lack may be due to sampling, because in the Haragan faunas there are fragments with narrower processes with a more convex ventral surface that would fit Type B.

Having removed the *purduei* group from the Haragan collection, there remain 4 previously named groups—*taffi, huntonensis, lingulifer,* and *oklahomae*—and 1 newly recognized but unnamed group. *Dalmanites taffi* is represented by a single pygidium and is not considered further. The remaining four can be recognized not only by their pygidia but also by their cephala. Three of the pygidia fall readily into the types listed above; *huntonensis* is Type A, *lingulifer* and *oklahomae* are Type B, but the unnamed one has a mixture of Type A and Type C characters. It is possible that *lingulifer* and *oklahomae* should each be paired with 1 of the other 2 to make 2 dimorphs. They are all represented by several specimens, and an examination of their geographical distribution could give a clue as to which pairs should be associated. Unfortunately, no definite answer emerges, probably because of the lack of control on stratigraphic position. For example, all four occur at Old Hunton Townsite.

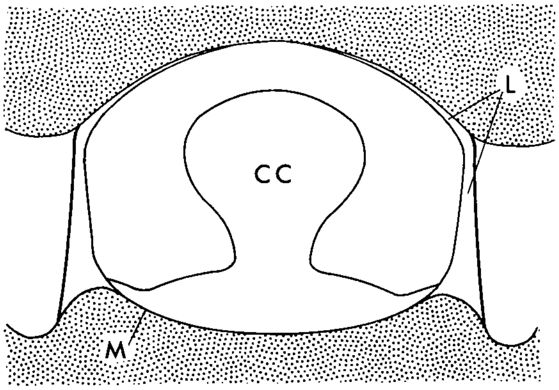
The position is so indefinite that it is thought unwise to recognize any hypothesis about dimorphism in the nomenclature of these forms. The established "species" names are therefore retained, but the newly recognized "species" is described but not named. Only controlled sampling holds hope of solving this problem.

Lens structure in certain Silurian-Devonian dalmanitinids

Huntonia (Huntonia) lingulifer

One vertical and two oblique polished sections of one eye of USNM 208986 are available. Partial recrystallization of the body of the lens has taken place, but some internal detail is preserved. The sclera is apparently unaltered.

The lenses tend to be cylindrical, with the external surface more convex than the internal. The average proportions are shown in text-figure 19. The corneal membrane is clearly preserved and is moderately thick. It



Text-figure 19. Semidiagrammatic medial section of lens from calcareous specimen of *H. (Huntonia) lingulifer* (Ulrich and Delo). For explanation of symbols, see text.

has an angular break in direction as it enters the sclera and forms a vertical cylinder around the lens, penetrating to the base of the sclera. Lining the inside of this cylindrical part of the scleral membrane is a layer of tissue (L) that is similar in appearance to the sclera and that continues around the inner surface of the corneal membrane on the upper lens surface. This layer is either quite attenuated or is absent across the middle part of the lens. Around the basal surface of each lens is a layer (M) that is approximately the same thickness as the cornea and appears to abut the sclera laterally.

Within some of the lenses a central core (CC) can be distinguished, usually by a slight change in color of the calcite. At one site the base of this core has been removed and replaced by matrix. Consequently, one can be confident of its reality and its overall shape. The whole central core is mamelonlike in form. Its base is close to, or touches, the basal covering layer (M), and its crest lies well above the level of the surrounding sclera.

Huntonia (Huntonia) purduei purduei

There are five specimens of this species (USNM 143113B-C, 1443089, 208982D 2 specimens) showing at least part of the eye preserved as silica. Molds of the external and internal surfaces are available as well as various replacements of the internal structures of the lenses (see pl. 19, figs. 1-3).

The external lens surfaces are moderately convex, rising well above the narrow, gently convex sclera. Each lens site is surrounded by a cylindrical sheath of silica (S). At its base this sheath is joined to the matrix forming the internal mold, but it is apparently continuous around the external surface of the lens. This continuity is not completely clear, but at a few locations the outer part of the external surface, at least, is formed of this layer. Inside this sheath, and separated from it by a gap (G) that is of comparable thickness to the sheath itself, is a mass of silica that is either hard and dense, or soft and rather porous. Where it is hard, it has a domed upper surface (D), separated from the external surface (S) by a narrow gap (G), which has been observed to be continuous with the gap inside the cylindrical sheath. This usually results in the main body of the lens coming away from the external surface when the specimen is fractured. However, at some sites there is enough silica crossing this gap to cause the replaced lens to fracture lower down. This suggests the possibility that the gap is not continuous over the whole lens surface.

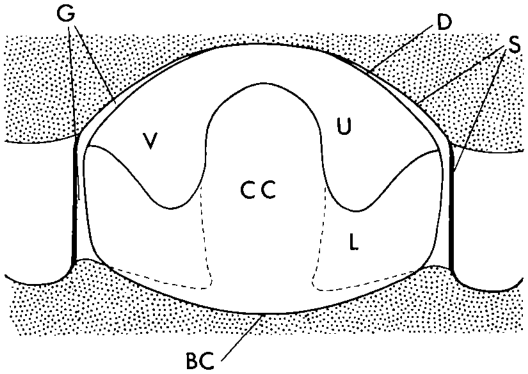
At the sites where the main body of the lens has been replaced by soft, porous silica, its upper part may be brushed away to reveal a craterlike surface (V) with a prominent central core (CC). The rim of this crater extends up to the level of the surface of the sclera, but the core reaches a little higher at some sites. Where it appears to be lower, it is probably poorly silicified or broken.

The surfaces of this craterlike structure are rarely smooth, presumably reflecting irregularities in the growth of the silica, but possibly also reflecting roughness of an original surface or even the partial removal of some of the soft siliceous replacement. Where the top of the central core is broken, it is either filled with solid silica or partly filled with soft fibrous silica.

At some sites, only a smooth basal cup (BC) is preserved. This is evenly curved, or it has a slight median depression, or it has the base of the central core still attached to it. This presumably means that the central core is normally not directly in contact with the basal cup, but that occasionally the layer between the two is silicified. The shape of the lower part of the central core is indefinite on all specimens, and the outline is therefore shown with a dotted line on the accompanying figure (text-fig. 20).

At some sites the basal cup is slightly roughened. It is difficult to know if this represents the silicification of a thin layer covering the cup or merely irregular silicification of the cup itself. On the accompanying diagram (text-fig. 20), this structure is shown as a distinct layer that expands into the base of the central core, but this interpretation has been influenced by observations on *H. (H.) lingulifer*.

Interpretation.—It is assumed that the lens structure in these two species will be sufficiently similar for one to be interpreted in terms of the other. The relationships in *lingulifer* indicate that the layer (S) of *purduei* is the corneal membrane and that the gap (G) is left by removal of the layer labelled (L) in *lingulifer*. So far as can be determined, this layer has the char-



Text-figure 20. Semidiagrammatic medial section of lens from partly silicified specimens of *H. (Huntonia) purduei purduei* (Dunbar). For explanation of symbols, see text.

acteristics of sclera, and therefore its presence over at least an outer annulus of the lens is of great importance. The sclera is thought to absorb light, and consequently the annulus around the lens surface would act as a diaphragm, admitting light only around the lens axis.

The crater surface (V) of *purduei* has no equivalent in the specimen of *lingulifer,* in which it may have been lost as a result of recrystallization; alternatively, the surface (V) may be an artifact, as has been explained previously. It is assumed to represent the contact between two lens elements (U and L), which are probably the homologues of the upper unit and the intralensar bowl of the phacopid lenses described by Clarkson.

The lenses of both species are cylinders with convex upper and lower faces. The same is true of the Silurian *Dalmanites imbricatulus* Angelin figured by Lindström (1901, pl. 3, figs. 43-44), and the Silurian *Odontochile meridianus* (Etheridge and Mitchell) from Yass, New South Wales, which I have examined. The former species also shows the cylindrical layer inside the corneal membrane arching up inside the cornea on the external surface, but the available material of the latter is not well enough preserved to show this. It is possible, therefore, that these are features of Silurian-Devonian dalmanitinids in general.

Other than the presence of the central core, upper unit, and intralensar bowls, there are few similarities between these lenses and those of contemporaneous Phacopidae, and there are almost no close comparisons between them and the only described Ordovician dalmanitacean lenses (Clarkson, 1968). Their origin remains obscure.

Aspects of functional morphology

1. *Cephalic-pygidial contact on enrollment.*—Clarkson and Henry (1973) recently showed that some dalmanitaceans, such as *Crozonaspis* and *Kloucekia,* make tight cephalic-pygidial seals when the animal is completely enrolled. Such junctions are effected by the development of vincular furrows and cephalic processes that fit into cavities in the pygidial doublures. These structures have been termed coaptative. Presumably they permit complete protection of the soft parts.

Silurian and Devonian dalmanitinids rarely, if ever, show such features. On the contrary, the doublures of cephalon and pygidium tend to be flat or inclined and do not show furrows of any kind. In anterior view, the cephalic doublure of most Silurian species of *Dalmanites* makes a broadly sinuous curve (see Campbell, 1967, pl. 17, fig. 9), whereas the pygidial doublure, in posterior view, has a simple curve that is not complementary. With the lateral margins of cephalic and pygidial doublures in contact, a small slitlike gap is left on each side of the sagittal line. Most of the soft ventral surface is thus protected, but macroscopic predators could enter via these slits. What then is their function? There are two possibilities:

a. The doublure shapes have some function related to the outrolled animal, and the slits produced at enrollment are an incidental byproduct. The negative selection for open slits is more than balanced by the positive selection for the doublures when the animal is outrolled.

b. The slits have a positive value, and this may be related to the entry of water-bearing food and oxygen, the exit of feces, and (or) protrusion of soft parts such as the antennae, while the animal was enrolled.

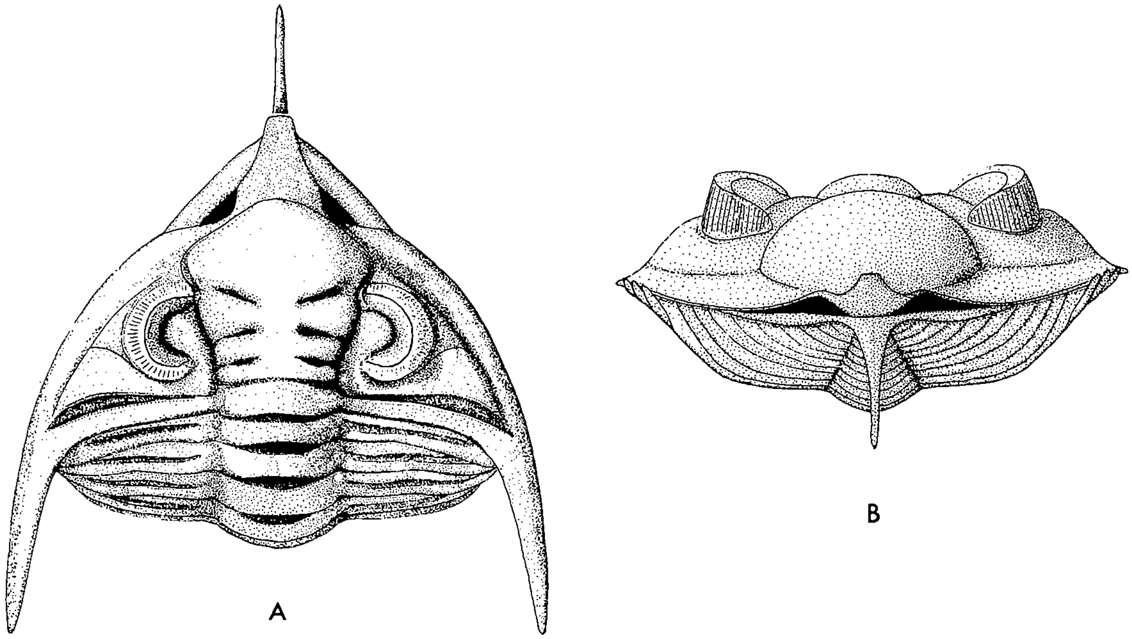
The former view is unlikely, because slits are produced by animals having variations in pygidial and cephalic outlines, in the number of pygidial rings (and hence pygidial limbs), and in widths of doublures. It is difficult to believe that among this variety none would have produced the minor pygidial deflections necessary to complete the seal if this had been of positive value. In fact, the opposite seems to have happened, and in some stocks the size of the slit is increased in various ways, or the number of slits is multiplied. This very multiplicity demonstrates positive selective value of the slits and induces an attempt to find explanations like those offered in b above.

Members of the Dalmanitidae in the faunas under discussion in this bulletin exhibit three different modes of increasing the area of these slits (see text-figs. 21-23), and they will be referred to by the names of the genera or subgenera in which they are characteristically developed.

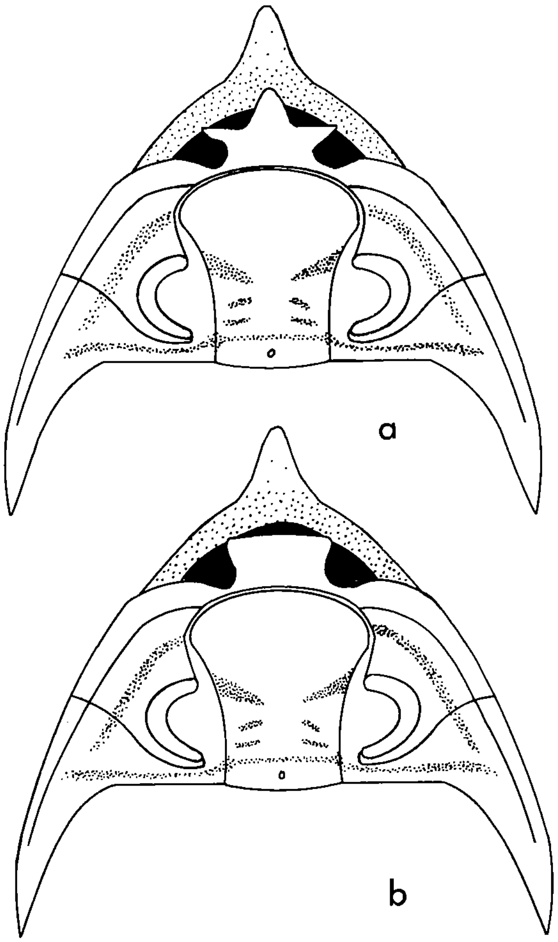
The *Huntonia* mode is nicely exhibited in a specimen of *H. (H.) lingulifer*, which is in a state of undistorted enrollment, though its margins have been destroyed (see pl. 20, fig. 1a). The depression in the posterior extremity of the pygidial doublure is neatly met by the ventral surface of the anterior cephalic process at the point where it becomes abruptly narrower. This forward position of the pygidium, together with the embayments in the cephalic border lateral to the base of the process, adds a horizontal dimension to the slits, the dorsad deflection of the border being retained. Although *lingulifer* is the only species that has been found enrolled, all species of *H. (Huntonia)* have similar structures and hence are assumed to have functioned in the same way.

The *Prosocephalus* mode is characterized by more than one slit on each side of an anterior cephalic process. Although no enrolled specimen has been found, it is clear from the matching of pygidia and cephala that the tip of the anterior process of *H. (Prosocephalus) xylabion* fits against the posterior extremity of the doublure, leaving two openings on each side. Structures similar to this mode developed independently in synphoriinids such as *Synphoroides biardi*.

The *Phalangocephalus* mode is characterized by the presence of more or less horizontally directed spines around the cephalic margin and by a pygidium on which the only spine is terminal. No enrolled specimens have been found, but from the matching of the shapes of the cephalon and pygidium, it



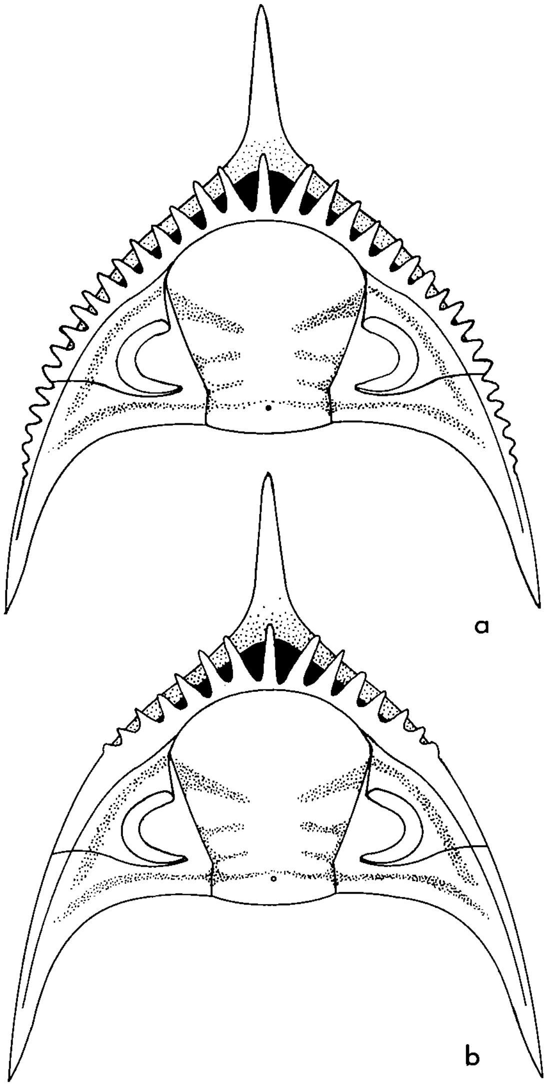
Text-figure 21. Reconstruction of dorsal and anterior views of *H. (Huntonia) lingulifer* (Delo) to show relationship of cephalon to pygidium during enrollment, and gaps lateral to base of anterior cephalic process.



Text-figure 22. *a*, reconstruction of dorsal view of specimen of *H. (Prosocephalus) xylabion*, new species, at complete enrollment. Note gaps produced by tridentate form of anterior cephalic process.

b, similar view of *H. (Prosocephalus) palacea* (Savage, 1913) in which 3 gaps are produced rather than 4. These two types are concerned to be representative of *Prosocephalus* mode.

is concluded that the pygidial margin met the ventral surfaces of the spines on the anterior and anterolateral part of the cephalon. In these positions, numerous slits between the spines would have been left open. It is interesting to note that on *P. rutabulum*, spines are present around this part of the cephalon only, whereas in *P. dentatus*, they extend as far back as the genal spines, where none could possibly be in contact with the pygidium, and some may even be too far back to meet the tips of the enrolled thoracic segments. Thus, the spines are unlikely to have been developed to serve only one function. *Odontocephalus* is a synphoriinid that developed a similar set of marginal structures. Its border is deeply di-



Text-figure 23. *a*, reconstruction of dorsal view of specimen of *Phalangocephalus dentatus* (Barrett) at complete enrollment.

b, similar view of *Phalangocephalus rutabulum*, new species.

Note overlap of cephalon by pygidium, and failure of denticles on lateral part of cephalon to come into contact with pygidial doublure in *P. dentatus*.

vided into a series of spatulate extensions that are almost contiguous at their distal tips, leaving narrow slits between. An enrolled specimen of *O. selenurus* (Eaton) figured by Hall and Clarke (1888, pl. 12, figs. 10-11) has the outer edge of the pygidium against the outer edge of the cephalic spines. Since the doublure of the pygidium is inclined, each slit in the cephalic border serves as an opening into the space between the pygidium and cephalon. In *Odontocephalus* the cephalic spines occur only on the front part of the cephalon. The pygidium has a pair of posteriorly directed spines at its posterior end, but the border between them is apparently not dorsally arched. These spines may have served a sensory function, or they may have been for stability.

Corycephalus probably represents a fourth mode, but the genus is poorly known. It is probable that its ventrally directed marginal cephalic spines either met the flat doublure of the pygidium to produce a portcullis-like structure, or the pygidium lay within these spines and the slits between the spines could be varied in size by the raising or lowering of the pygidium against their inner surfaces. However, this is sheer speculation.

Finally, it is noted that an opening is produced in the synphoriinid *Coronura* by a method quite different from that found in any dalmanitinid. The cephalon in this genus has an unmodified anterior border, but the pygidium has a terminal embayment which is also arched dorsally. At the position of maximum enrollment, this leaves an open tunnel into the cephalo-pygidial chamber, and this varies in dimensions from species to species (see Lespérance, 1975). It is of interest that there is a posteriorly projecting spine on each side of this tunnel, but these spines are shorter than those on *Odontocephalus* in which no tunnel is present. In addition, there are numerous fine spines around the pygidial margin.

Interpretation.—The small multiple openings in *Odontocephalus* and *Phalangocephalus* could not allow the extrusion of the antennae while the animal was enrolled, nor are they arranged in the most advantageous way to dispose of the feces from the anus. On the other hand, they would be well suited to allow the controlled passage of water. The spines carry numerous perforated granules, and these may have been the sites of chemosensory and (or) tactile organs to monitor, and perhaps filter, water passing in and out. If it is concluded that passage of water was one of the primary functions in animals of this type, it is possible to extend this interpretation to less obvious examples such as *Huntonia.* The means of monitoring the water flow and protecting the open slits in such forms are less effective than in *Odontocephalus,* as increase in slit area can be brought about only by enlarging the slit as in *H. (Neoprobolium)*, or by dividing the process as in *H. (Prosocephalus).* It may be possible to explain the bifid or trifid tips on the process of *H. (Neoprobolium)* in terms of a monitoring system. The general direction of the incurrents will be posteroventral; that is, water will flow over the anterodorsal surface of the process on each side. In order to monitor this water, the tip of the process becomes divided, and the tips turn dorsolaterally. Similar monitors are known to exist in living crustaceans such as the crab *Corystes cassivelaunus,* in which the antennae perform the dual roles of tube formers and sensors when the animal is buried. It is interesting to note that *H. (Huntonia),* which has a simple process or one with a rudimentary division of the tip, has a narrower intake area. *H. (Neoprobolium)* is a development that exploited a wide intake area and hence has had to produce a more efficient monitory system. The presence of paired spines on the pygidia of *Odontocephalus* and *Coronura* offers added support to this hypothesis.

The water-flow hypothesis may not be the only explanation of these openings. In *Coronura,* the tunnel is ideally placed to remove the feces, and it may also have served for the exit of the antennae. The slits in *H. (Huntonia)* are also well situated for the latter purpose. However, these seem to be secondary functions.

It is now necessary to show that the flow of water into the cephalo-pygidial chamber would be of some benefit to the organism. With the limbs in close juxtaposition during enrollment, very little filtering of food particles or oxygen exchange could take place on the filaments of the exites. However, the appendages on the cephalon and the large flat pygidium would be less affected than those of the thorax, and both feeding and respiratory functions could have been maintained at a reduced level during enrollment. Thus, the development of all these structures for water passage may be regarded as adaptations to enable the animals to remain enrolled for protracted periods, presumably while they were in danger of predation.

2. *Antennal furrows.*—There is a shallow arcuate furrow in the doublure in front of the hypostomal suture in all species of *Huntonia*. This is in no way comparable with the vincular furrow of phacopids. If the hypostome is restored to its life position, the furrow is seen to cross the suture just above the anterior wing, i.e., at the front of the antennal notch. A similar furrow is found in *Dalmanites* and *Odontochile,* but it is not present in tightly enrolled forms such as *Kloucekia.*

The interpretation of this furrow is largely a matter of conjecture, but its constant relation to the hypostomal suture and antennal notch, and the evidence that it seems to occur only in dalmanitaceans that do not make a tight seal on enrollment, suggest the possibility that the antennae lay crossed over in this furrow when the animal was enrolled. In this position they would leave room for the pygidial appendages to function in respiration when conditions were suitable, and yet be able to flex forward to adopt their normal sensory function with the animal only minimally unrolled.

3. *Pygidial segmentation.*—One of the more obvious features of dalmanitinid evolution is the increase in the number of pygidial segments from the Silurian to the Devonian, and this numerical increase is accompanied by an increase in pygidial size. This may imply that there is an optimal segment size and that a species cannot increase its total body size beyond certain limits without adding more segments. The optimal size may in turn be controlled by the need for an increased number of appendanges both for locomotion and respiration. It would be more efficient physiologically and more feasible mechanically to increase the area of the respiratory surfaces by adding new exites, rather than increasing the size of the existing ones. Beyond a certain length, the filaments could not be accommodated during enrollment, and beyond a certain thickness their exchange efficiency would be diminished. Consequently, the increase in pygidial segmentation in the *Dalmanites-Odontochile* transition is probably to be explained, at least in part, as the result of a general increase in adult size.

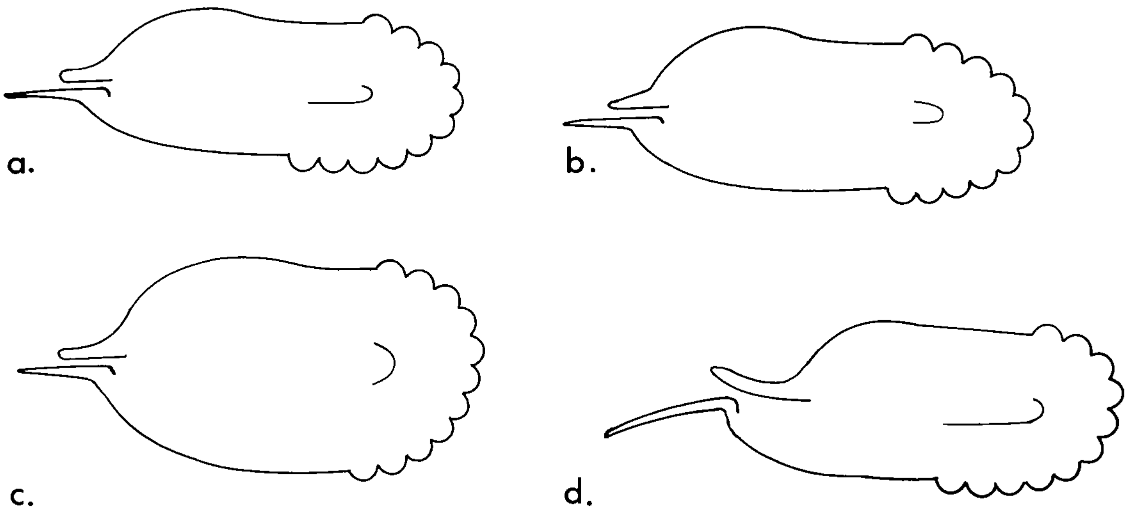
But the increased area for respiration on the pygidial appendages had an added significance if the animal had to respire for long periods during enrollment. As indicated above, this was probably a feature of members of the Dalmanitinae. The pygidial appendages would be minimally affected by enrollment, and provided there was sufficient convexity of cephalon and pygidium, they should be able to maintain water circulation, though with reduced efficiency. It would thus be to the advantage of the animal if the length of the pygidium, and hence the number of segments, were increased.

4. *Thorax and enrollment.*—Because dalmanitinids are not commonly found enrolled, little has been written about the morphological features that control their enrollment patterns. Nevertheless, the fact that taxa are diagnosed on the shapes of doublures and marginal flexures means that enrollment is indirectly (and often unconsciously) being used. Recently Clarkson and Henry (1973), Bergström (1973), and Campbell (1973) have all commented on various aspects of enrollment in dalmanitaceans, and it has become obvious that more attention to this feature is needed if there is to be a rational taxonomy of the group. For example, it is difficult to accept that *Kloucekia,* which enrolls like a phacopid (Clarkson and Henry, 1973), should be in the same subfamily as *Dalmanitina*, which enrolls like a dalmanitinid.

A good indication of the nature of enrollment in the *Dalmanites* group is given by the specimen of *H. (Huntonia) lingulifer* mentioned above. But even without this, taking into consideration that the more or less planar cephalic and pygidial doublure surfaces have to be juxtaposed at full enrollment, and that all dalmanitinids have 11 thoracic segments, there is a limited number of possibilities. These are controlled by several factors: the combined convexities of the cephalon at its posterior end and the pygidium and its anterior end; the amount of overlap of the anterior of the cephalon by the pygidium on full enrollment; the length of the thoracic segments with respect to the length of the animal; the extent to which the axis of the pygidium extends in front of the position of maximum pygidial width. Of these, only the first three are of consequence; the others show little variation between species. The effects are shown diagrammatically in text-figure 24.

This analysis suggests that species of *Dalmanites*, which are rather flat and have relatively short pygidia that do not overlap the front of the cephalon at full enrollment, should have a very high maximum thoracic flexure situated well forward. Species of *Odontochile*, with their strong convexity and relatively long pygidia that also show no cephalic overlap, should have a more even flexure, but the maximum should be toward the middle of the thorax. Most species of *H. (Huntonia)*, which have pygidia of intermediate length that *do* overlap the cephalon and also have intermediate convexity, should vary in shape with changes in these factors. Some species of *H. (Huntonia)*, such as *purduei*, which have very long pygidia and little overlap, should be closer to *Odontochile*. Unfortunately, I have access to only one enrolled specimen, *H. (H.) lingulifer*, but it does conform to the prediction.

However, there is another method of checking this hypothesis. Many trilobites, including the dalmanitinids, show an increase in the width of the axial rings of the thorax toward the mid-length. However, there is variation in both the position of maximum width and in the degree of widening, i.e., the ratio of maximum/minimum width. Values for seven species are given in table 4. They have been taken from specimens thought to be only slightly distorted, if at all; but the photograph by Horný and Bastl (1970, pl. 17, fig. 7), together with Barrande's drawings, have been used for *O. hausmanni*. It is impossible to give a precise estimate of the order of accuracy involved, but it is probably about 2 percent. In summary, these figures show that the species of *Dalmanites* have the highest variation in widths and that the maximum width is well forward of the middle segment; *Odontochile* shows the least variation in widths, and the maximum width is around the middle segment; species of *H. (Huntonia)* with tails of intermediate length and a forward enrolled posterior fall between these extremes but are closer to the *Dalmanites* species, whereas *purduei*, with its long tail placed



Text-figure 24. Schematic diagram of longitudinal median sections of enrolled dalmanitaceans with 11 thoracic segments of uniform size, to show effects on enrollment of varying length and height of cephalon and pygidium, and amount of overlap of cephalon by pygidium.

a, situation in *Dalmanites* with weakly convex cephalon and pygidium, and relatively short pygidial axis.

b, and *c*, situation in *Odontochile* with more highly convex cephala and pygidia and relatively longer pygidia.

d, situation in *Huntonia (Huntonia)* with cephalon and pygidium of moderate convexity and pygidium effectively shortened by its forward position relative to cephalon.

farther back with respect to the head when in the enrolled position, is closer to *Odontochile*. (Note that the narrow posterior rings in *Dalmanites* cannot be explained by suggesting that the small number of pygidial rings requires a high rate of decrease in ring width in the thorax. Many species of the genus show a "waisted" pygidial axis, demonstrating that there is no difficulty in contracting the axial width in less than 10 rings.)

Thus, these results indicate that high variability in ring width and position of maximum ring width are correlated with both the predicted unevenness of enrollment and the position of maximum flexure. Such features may therefore be of significance in taxonomic studies.

A possible functional explanation could be that widening results from an attempt to increase the space inside the axial region at positions where compression of organs would be greatest because of maximum skeletal flexure.

5. *Apodemes and musculature.*—Similar cephalic apodemes to those of *Dalmanites puticulifrons* figured by Whittington and Campbell (1967, pl. 14, fig. 4; pl. 19, fig. 15) have been observed in other species of *Dalmanites* and *Huntonia* and may be regarded as representative of the subfamily. The occipital apodeme is transverse dorsally, but it is rotated so that its ventral edge lies at about 45° to the sagittal plane of the animal. It has a concave face directed posterolaterally. Apodeme 1p tends to become subtriangular in cross section toward its ventral end, with the broadest face (which is slightly concave) directed posterolaterally. Apodeme 2p remains transverse and almost planar and is slightly concave on its posterior face (see pl. 4, fig. 4).

About two-thirds of the pygidial segments have apodemes; the remainder seem to have merely muscle attachments. The ventral edges of the apodemes are deepest axially and arch up evenly to the dorsal furrow, successive apodemes thus forming a longitudinal arcade. The width of the apodemes decreases on successive segments, and the last one is usually just a spike. One important feature is the presence of a small concave area on the anterior surface of each apodeme (see pl. 4, fig. 3).

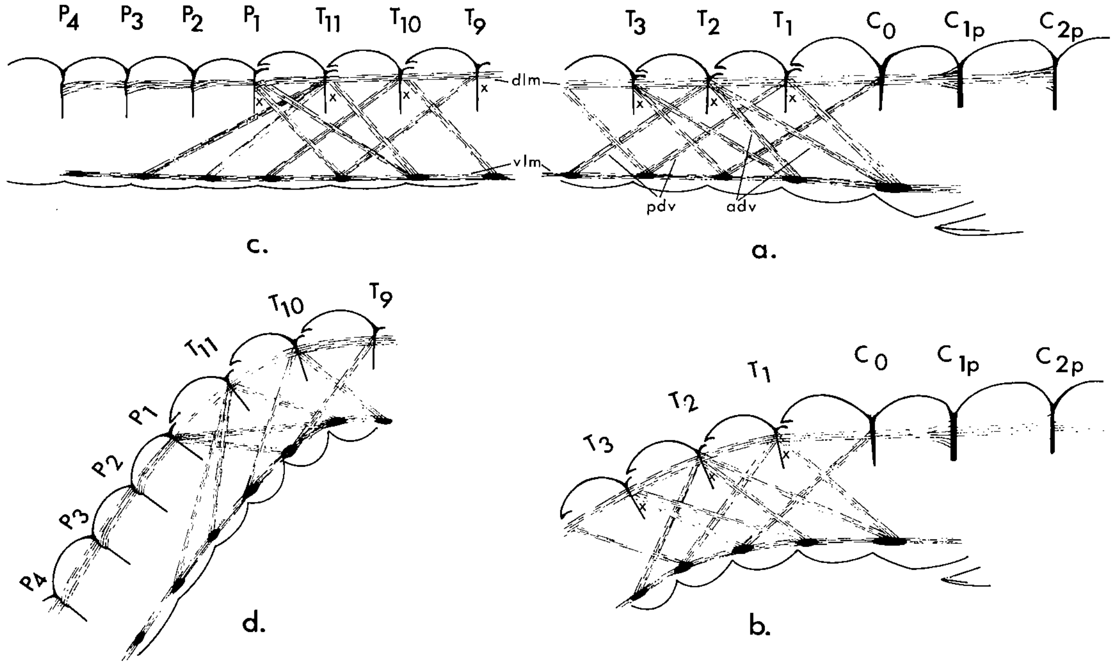
There are other muscle insertions on the main parts of the pygidial rings behind the apodemes, at least in species of *Huntonia*. These appear on the external surface as 1 to 3 shallow, unornamented pits on each side of a ring (see pl. 21, fig. 1a; pl. 22, figs. 4, 5). On the internal surface they appear as slight, irregular rugosities (see pl. 26, figs. 5, 6) lying directly behind the apodemes, but not on either side. They may be present on the rings without apodemes at the posterior end of the pygidium, but if so they are very weak.

TABLE 4.—NORMALIZED RELATIVE WIDTHS OF FIRST AND LAST THORACIC RINGS OF SELECTED DALMANITINID SPECIES

	Width of first thoracic ring	Width of widest thoracic ring	Width of last thoracic ring	Number of widest ring
D. limulurus	94	100	73	3-5
D. rutellum	-	100	75	3
H. (H.) lingulifer	91	100	77	4-6
H. (H.) huntonensis	93	100	77	3-6
H. (H.) oklahomae	93	100	80	3-6
H. (H.) purduei	-	100	84	3-6
D. hausmanni	95	100	87	3-7

The thoracic apodemes are not well known in any species with which I am acquainted; they are much less robust than those on the pygidium, and on *H. (H.) purduei* at least, they have a slight transverse concavity high up on both anterior and posterior surfaces. There are also muscle insertions into the thoracic rings similar to those on the pygidial rings.

The concavities on the apodemes suggest points of muscle insertion, and it is highly important, therefore, to notice that those on the cephalon face backward, those on the pygidium face forward, and those on the thorax face in both directions. Some of the muscles attaching at these positions would have been the dorsal longitudinals that are found in most primitive enrolling anthropods (Hessler, 1964). These usually form a sheet directly beneath the axial region of the dorsal exoskeleton and attach either to a rim on each segment or to a suspensory tendon. They enable the animal to outroll (or flex). In dalmanitinids they probably passed through the smooth arcades on both the adaxial and abaxial sides of the thoracic and



Text-figure 25. Semidiagrammatic longitudinal sections through apodemes of dalmanitinid trilobite to show arrangement of muscles involved in enrolling and outrolling animal. Drawn to scale.

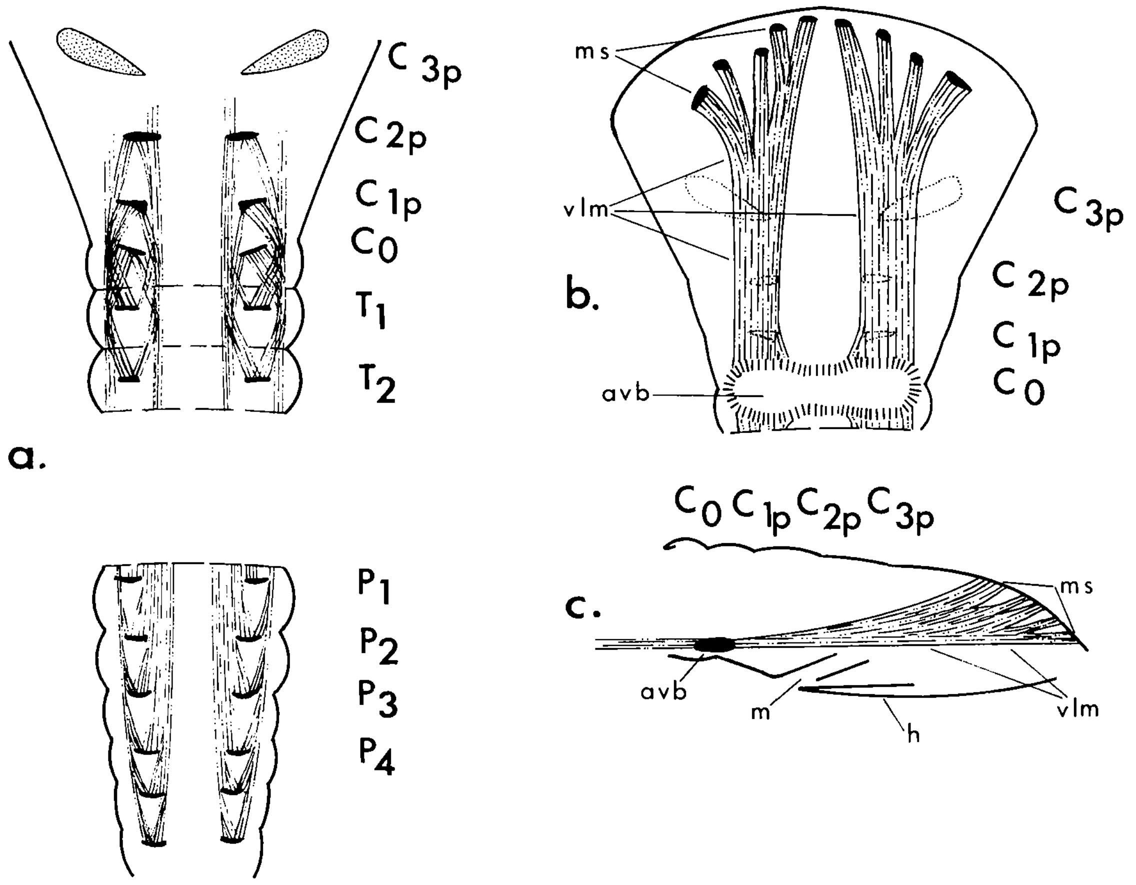
a, b, relaxed and partly enrolled specimen sectional along posterior of cephalon and first three thoracic segments.

c, d, relaxed and fully enrolled specimen sectioned along last 3 thoracic segments and first 4 pygidial segments.

adv, anterior dorsoventral muscles; *dlm,* dorsal longitudinal muscles; *pdv,* posterior dorsoventral muscles; *vlm,* ventral longitudinal muscles; *P1-4,* pygidial apodemes; *C,* cephalic apodemes; *T1-11,* thoracic apodemes.

pygidial apodemes, but the bulk of the fibers were probably on the abaxial side. This may explain why the attachment faces of the occipital and 1p cephalic apodemes are directed posterolaterally and 2p is directed posteriorly. The enlarged attachment face on 1p is probably to be explained as an anchor post, as there are only three attachment sites in the cephalon, which is a large structure with high inertia. The pygidium, which is almost as cumbersome as the cephalon, and which would have to be rotated against the resistance of the surrounding water, has a large number of attachments extending back about two-thirds of its length. As can be seen from text-figures 25c and d, the dorsal longitudinals are virtually the only effective muscles available for outrolling the pygidium, and hence the need for a large number of attachment points. If we make the assumption that ventral endoskeletal bars existed in the thoracic and in the first few pygidial segments as they do in most primitive enrolling arthropods, another possible outrolling muscle would be an anterior dorsoventral muscle attached to the apodeme P1. (In the figure, I have shown two muscles attached to P1, to indicate how added force may be exerted, though according to Hessler it is not normal for these muscles to extend across more than one segment.) As can be seen from text-figure 25d, anterior dorsoventral muscles that were attached to P2 or subsequent apodemes would pass below the fulcral point of the first pygidial segment, and hence *enroll* the pygidium. It is unlikely, therefore, that any such muscles existed.

On the other hand, anterior dorsoventral muscles would have been effective in enrolling the inter-thoracic and cephalothoracic joints, as is shown on text-figure 25. These muscles also attach into the concavities on the front of the thoracic



Text-figure 26. *a*, schematic dorsal view of axial region of posterior of dalmanitinid cephalon, first 2 thoracic segments, and first 6 pygidial segments to show arrangement of dorsal longitudinal muscles.

b, ventral view of cephalon, showing ventral longitudinal muscles, ventral cephalic bar, and attachment of muscles into anterior lobes of glabella.

c, lateral view of head, showing same features, together with hypostome in position. Anterior end not complete.

Symbols as in previous figure, plus *abv*, anterior ventral cephalic bar; *h*, hypostome; *m*, mouth; *ms*, muscle scars.

apodemes. The cephalic ventral endoskeletal bars must have been posteriorly situated, because on all dalmanitinids the hypostome extends well back. Muscles are shown extending from the cephalic bars to apodemes T_1, T_2, and T_3, to show that they could have been effective in all these positions, though this does not guarantee their existence.

Enrollment would presumably have been achieved, as in other primitive arthropods, mainly by the contraction of ventral longitudinal muscles. They would have been attached to the ventral bars in the various segments, and these are not preserved. However, as can be seen from text-figures 25 and 26, they must have been anchored to the front wall of the cephalon in order to be effective. Thus, at least some of the muscle scars interpreted by Eldredge (1971) and previous workers as sites for the attachment of hypostomal and visceral suspensory muscles were for the anchorage of the ventral longitudinals. This view is supported by the fact that in some species, e.g., *H. (Huntonia) purduei fittstownensis*, the anterior glabellar lobe is locally distorted in the region of the scars, as though strong stresses had been exerted before the exoskeleton had become rigid. The bilateral pattern of the scars is also consistent with this view. The other possible enrolling muscles are the posterior dorsoventrals, and there is some positive evidence of their existence. They would attach to the posterior faces of the thoracic apodemes but would not be present in the pygidium. The presence of cavities on the back of the thoracic apodemes and their absence on the back of the pygidial apodemes is good evidence that these muscles were present. Two are shown in text-figures 25c and d attached to apodeme T_{11}, to show that they could both be effective. In the cephalon the only one shown is attached to the occipital apodeme, though there could have been others attached to 1p and possibly even 2p.

As an inspection of text-figure 25 shows, the enrolling muscles all exert large moments around their respective fulcra. By contrast, the outrolling muscles all operate on very short levers and exert comparatively small moments. This comment is particularly applicable to the moments across the cephalo-thoracic and pygidial-thoracic joints. The strength of the argument is undiminished even if the presence of a system of external dorsal muscles (Campbell, 1975, fig. 2) connecting the articulating half rings with the next anterior segments is accepted. Because of the low convexity of the axial rings, such muscles would also be able to exert only small moments. It may be concluded, therefore, that these animals could enroll rapidly and resist considerable stresses exerted by predators attempting to open them, whereas they could outroll themselves only gradually.

The muscle scars on the rings themselves are appropriately situated for the attachment of the dorsoventral muscles and for the appendage muscles. It is improbable that they were for the dorsal longitudinal muscles, because they extend to segments so far back on the pygidium and because on the pygidium they are separated by deep apodemes that would obstruct their passage. An organism such as a dalmanitinid would, if it functioned in the manner suggested, require strong dorsoventral muscles to maintain the ventral intersegmental bars in position. Further, some of the scars are situated well in toward the axis, whereas the extrinsic limb muscles in primitive arthropods are attached in a more lateral position (Hessler, 1964, p. 33). It is impossible to be definite, but in the light of the above evidence the scars on the rings are interpreted as the attachment sites of both dorsoventral and appendage muscles. Some of the latter must also have been attached to the tips of the apodemes.

Genus **Huntonia**, new genus

Type species.—Dalmanites lingulifer Ulrich and Delo, from the Haragan Formation.

Diagnosis.—These are moderately convex dalmanitinids (in the sense of the above discussion) with a simple, bifid, or trifid anterior cephalic process. Pygidium has a caudal spine and enrolls so that the posterior end of the pygidial doublure meets the ventral surface of the anterior cephalic process at some distance from its base, leaving one or more open areas on either side; glabella is tuberculate or granulate; pygidium is usually granulate but also has a few irregularly scattered tubercles.

Subgenera assigned.—Huntonia (Neoprobolium) Struve, 1958, with type species *Asaphus nasutus* Conrad.

Huntonia (Prosocephalus), new subgenus, with type species *H. (Prosocephalus) xylabion,* new species.

Remarks.—This genus is based on the presence of a pronounced anterior cephalic process, a morphological feature that is interpreted as an adaptation to increase the amount of water flowing over the appendages while the animal was enrolled. The three constituent subgenera are defined mainly on the shape of this process, although there are differences in ornament, shapes of the cephalic borders and genal spines, and shapes of the pygidial spines. However, these subgenera share a large number of characters, they all could be formally derived from a *Huntonia (Huntonia)* morphology, and they all are restricted to the Appalachian Province, where they appear over a short period of time. Consequently, it seems best to regard them as a radiation from a single stock rather than as independently evolving lines. It is possible, however, that further information on such features as the hypostome and the nature of the dimorphism of *H. (Neoprobolium)* and H. (Prosocephalus) will require a reassessment of this view. It may even be impossible to establish that *H. (Huntonia)* itself is monophyletic.

As far as I am aware, this genus is restricted to North America. Clarke (1908) referred the European species *Dalmanites beyrichi* Kayser and *D. galloisi* Oehlert to *Probolium* (now *Neoprobolium*), but further work is needed before these assignments can be accepted.

The subgenera *H. (Prosocephalus)* and *H. (Neoprobolium)* are not likely to be confused with any other genera, but *H. (Huntonia)* shows similarities to species assigned to *Dalmanites*. This problem is dealt with in the discussion on the subgenus.

Subgenus **Huntonia (Huntonia)**
new subgenus

Type species.—Dalmanites lingulifer Ulrich and Delo, from the Haragan Formation.

Diagnosis.—Anterior cephalic process is simple, tending to be almost parallel sided posteriorly but convergent anteriorly; border is markedly contracted at the base of this process; cephalic doublure is narrow to moderately wide; hypostome is elongate, central body is flattened and it has short anterior wings and seven marginal spines. Anterior pleural tips on thorax are acute and almost straight; posterior ones become more scimitar-like. Pygidium has 14-22 axial rings and 11-16 pleurae; caudal spine is always present; pygidial doublure is narrow to moderately wide and is modified at the posterior extremity to lock with the anterior cephalic process on enrollment. Entire surface is granulate, or partly granulate and partly smooth. Dimorphism and trimorphism are exhibited in the size and spacing of the granules, the width and attitude of the cephalic and pygidial doublures and the anterior cephalic process, and the length and inclination of the caudal spine.

Species assigned.—Dalmanites lingulifer Ulrich and Delo; *Dalmanites huntonensis* Ulrich and Delo, *Dalmanites oklahomae* Richardson, *Odontochile purduei* Dunbar, *O. lindenensis* Delo, *O. acuminatus* Ulrich and Delo, and *O. dunbari* Delo.

Species probably assigned.—O. mississippiensis Delo, *Asaphus micrurus* Green.

Remarks.—The species placed in this new subgenus have been previously assigned to *Dalmanites, Odontochile,* or *Neoprobolium* (see Delo, 1940; Campbell, 1967, for summary). Recently Maksimova (1972) placed several of them in her two new subgenera and the nominate subgenus of *Odontochile. Odontochile purduei, O. dunbari,* and *O. micrurus* were placed in *O. (Odontochile)*; *Dalmanites lingulifer* was placed in *O. (Kasachstania)*; and *D. taffi* was placed in *O. (Reussia)*. On the other hand, Lespérance (1975) placed *O. dunbari* in *Forillonaria*. This gives some measure of the conflict of opinion over these forms. Much of the disagreement derives from the incomplete description of the species in question, but there has also been an over-emphasis on rule-of-thumb identification procedures. In my view, it is not possible to make a proper estimate of relationships simply on the basis of isolated pygidia or cephala.

The new subgenus can be distinguished from all other subgenera of *Huntonia* by the long, simple anterior cephalic process, combined with the contracted border at its base. The same features distinguish it from *Odontochile* and *Dalmanites,* though it is probable that a similar type of structure was evolved earlier in species commonly assigned to *Dalmanites,* such as *D. vigilans* Hall from the Silurian of Illinois and Wisconsin. Such species should be separated into a new subgenus if this estimate proves correct. *H. (Huntonia)* can also be distinguished from species of this type, as well as from species of *Dalmanites* s.s., by the greater number of axial rings and pleural furrows on the pygidium, and by the strongly denticulate hypostomal border. The hypostome is certainly reminiscent of *Odontochile,* though the anterior pair of lateral spines is situated farther forward than is normal in that genus. Species such as *Dalmanites rutellum* Campbell, from the underlying Henryhouse Formation, and *D. puticulifrons* Whittington and Campbell, from the Upper Silurian rocks of Maine, both of which have short, rounded anterior cephalic processes, are excluded from the genus, though they may well have been close to its ancestral lineage. They may be distinguished by the absence of a contraction of the border at the base of the cephalic process and by having fewer segments in the pygidium. No species of *H. (Huntonia)* has a pygidial doublure as wide as that of species referred to *O. (Reussia)* or O. (Odontochile) by Maksimova.

There are 2 groups of species included in the subgenus, 1 with 13 to 16 pygidial axial rings, and the other with 18 to 23. Although the number of rings is known to be of evolutionary importance in the transition from the dominantly Silurian *Dalmanites* to the Devonian *Odontochile*, the limiting number of axial rings having been arbitrarily placed at 16 by Delo (1940), I regard the development of the enrollment type indicated by the anterior process as a better indicator of relationships than the number of rings, which, as has been shown in the section on "Aspects of functional morphology," is probably mainly the result of an increase in animal size. However, it remains a possibility that these two groups achieved a *Huntonia* morphology independently.

Huntonia (Huntonia) lingulifer

(Ulrich and Delo, 1940)

Pl. 18, fig. 6; pl. 19, figs. 4, 5; pl. 20, figs. 1-4

Dalmanites lingulifer Ulrich and Delo; Delo, 1940, p. 45-46, pl. 3, figs. 29-30.

Holotype.—Delo (1940, p. 45) nominated the figured pygidium on his plate 3, figure 30, as holotype, but on the plate explanation (p. 122) he nominated the cephalon figured on his plate 3, figure 29. Since the former is the first mentioned, I accept it as valid. The specimen is now USNM 111557, and is labeled "Atoka Quadrangle, Oklahoma."

Diagnosis.—Cephalic profile is moderately convex; occipital ring measures 0.60-0.65 times the width of the anterior lobe; length of anterior lobe 0.60-0.65 times its width; anterior lobe is domed in anterior profile and moderately convex in lateral profile; preglabellar furrow is weak, with the facial suture lying in it laterally and just in front of it medially; anterior border is strongly contracted at the base of the anterior cephalic process; width of process at its base is about 0.80 times the width of the occipital ring, abruptly diminishing in width at about two-fifths of its length from the base; tip of process is strongly upturned and slightly bifid; upper surface is flat to slightly concave and lower surface strongly convex in transverse section; eyes have 37-38 files and a maximum of 9 lenses per file; subocular platform is narrow all round; free cheeks are almost vertical beneath the eyes anterolaterally; border is planar or has a faint epi-border furrow; genal spines are slender and extend back to the 5th or 6th thoracic ring; cephalic doublure is narrow; glabella is covered with rather uniform, moderate-sized granules. Thorax has fine granules similar to those of the cephalon. Pygidium is subtriangular; axis is poorly defined posteriorly; there are 14 complete and 1 incomplete axial rings plus terminal piece; 11 pleural furrows; terminal spine is narrow based, elongate, becoming almost circular in cross section distally, upturned at 30°-40° to the horizontal, and at least two-thirds as long as the pygidial axis; doublure is narrow with an inclined outer part that narrows toward the rear, and a steep high inner part that increases in height toward the rear; doublure is narrowly embayed posteriorly to take the anterior cephalic process on enrollment; dorsal surface has fine granules, those on the pleurae being finer than those on the axis; both anterior and posterior pleural bands are granulate.

Description.—Eight of the available specimens are sufficiently complete to make the association of heads and tails described herein certain. They include individuals ranging in glabellar length from 8.5 to 19.0 mm, covering much of the holaspid growth range. The largest of the isolated specimens is a pygidium with the axis 27 mm long.

The anterior glabellar lobe is moderately convex in both anterior and lateral profiles. The preglabellar furrow is faint and unornamented. In front of γ, the anterior limb of the facial suture converges on the lateral corners of the anterior lobe, and then it lies just within or just outside the preglabellar furrow before swinging out onto the anterior process. The anterior border is strongly constricted lateral to the base of the process, so that in dorsal view the glabella gives the impression of extending forward onto the base of the process. The subocular platform is always present and has basically the same form as that described for *huntonensis*, but it is invariably quite narrow. The cheek beneath it is almost vertical. Five eyes are well-enough preserved to permit a count of the files and maximum lens number, but not a total lens count. There are 37-38 files with a maximum of 9 per file. The 3 genal spines observed are slender, extend back to the level of the 5th or 6th thoracic ring, and have a terminal lateral angle of approximately 10°. The lateral border is narrow, and the epi-border furrow faint. Consequently, the outer part of the doublure is also narrow, never reaching more than 0.40 times the width of the occipital ring, and in some specimens it is as little as 0.33 times this width.

The glabellar ornament is of uniform size all over, consisting of granules 0.1-0.2 mm in diameter scattered at from 25 per square mm on the edges of the frontal lobe to as few as 8 on the median part of the lobe. There is similar ornament on the palpebral lobes and on the postocular fixed cheek. Away from these regions the granules become progressively finer. There is a sharp break in size from the palpebral lobe to the rim, the granules on the rim being half the size and more densely packed.

The thorax is better preserved than that of any of the other species of the subgenus. In average-sized specimens it shows the progressive increase in the length of the posteriorly turned pleural tips from zero on the first segment to 3 or 4 mm on the last. In an extended individual, a line joining the tips of the last pleurae would pass through the axis of the fourth pygidial segment. These pleural tips are flexed outward slightly as well as backward. The thoracic ornament consists of uniform granules like those of the glabella on the axial rings, with gradually weakening granules along the anterior and posterior pleural bands and then an increase again at the pleural ends. In the pleural furrows, there are numerous granules finer than those seen anywhere else on the exoskeleton. These are up to 0.05 mm in diameter and can be distinguished only on the best preserved specimens.

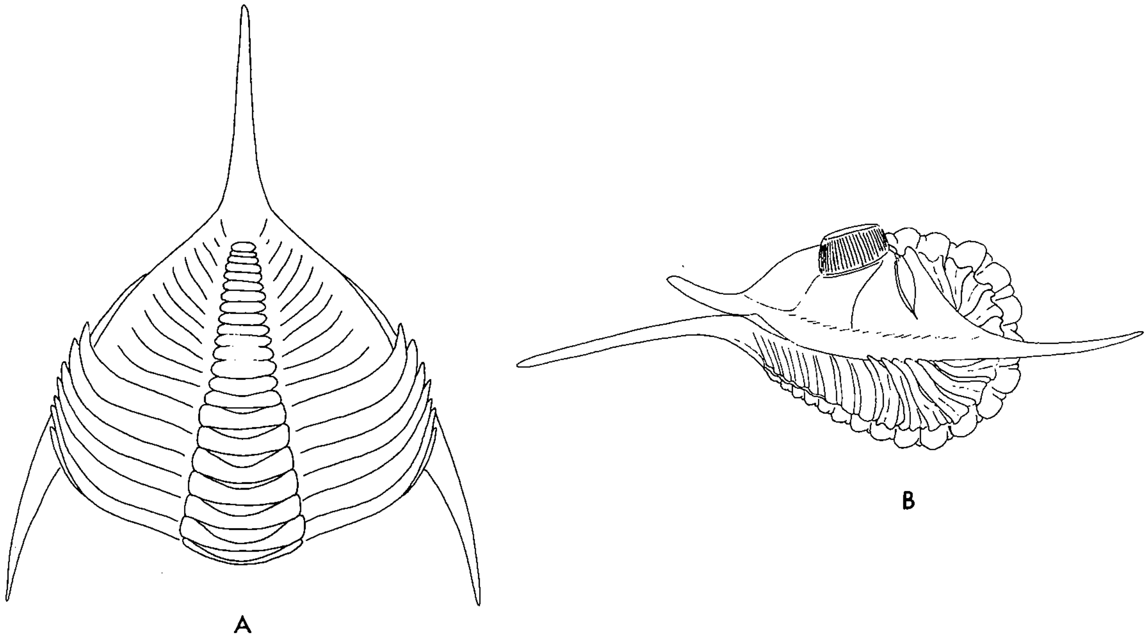
The pygidium is a typical Type B, with a subtriangular outline and upturned terminal spine. There are 14 complete and 1 incomplete axial rings plus a terminus, and 11 pleural furrows. The axis is poorly defined posteriorly, and the postaxial ridge is a broad, blunt-crested triangle in transverse section, curving up into the terminal spine from a point 1 or 2 mm behind the axis. The margins of the pygidium have a rather pinched-in appearance near the base of the spine. There are no complete spines, but one of the parts preserved is about 15 mm long (measured from the end of the axis) and gives the impression of being at least another 5 mm. This would make it about four-fifths as long as the pygidial axis. Where it is broken, it is an oblate ellipse in section, but it probably becomes more circular distally. Proximally, it is flat on the base. The outer part of the doublure reaches a maximum of about one-third the width of the first axial ring and shows a slight decrease in width posteriorly. The inner steep part is unusually high, being lowest toward the front and gradually increases in height toward the rear. A short distance in front of the spine it is higher than the outer part is wide. The angular junction between the two parts becomes less distinct posteriorly. There is a narrow but strong upswing of the doublure beneath the base of the spine. The ornament is similar to that of the thorax.

Remarks.—The holotype is an external mold of a pygidium with part of the terminal spine still in place. The surface detail has been largely removed, but enough of it remains for identification purposes. It is the second largest of the specimens available to me. Through the courtesy of Dr. F. Collier, I have been able to examine the paratype cephalon figured by Delo (1940, pl. 3, fig. 29), which clearly belongs to the same species. I have not examined the other two paratypes listed by Delo.

The range of variation within the species is small. The pygidium shows some variation in the width and proportions of the axis. In particular, the older specimens appear to have proportionately wider axes with blunter termini. There is also some apparent variation in the attitude of the outer part of the doublure, but this could be due to flattening of some specimens.

Three points in Delo's description need correction. The whole of the surface of the cephalon is granulate: the borders are not smooth. *All* the "ribs" show a definite interpleural furrow, which runs from the axis to the border. Their apparent absence on some specimens is due to slight wear of the surface. The granulation of the pleural furrows does not consist of "an irregular row" but is rather an irregular mass of granules so numerous that they could not be conceived of as being in a row. There is no linear pattern.

It is possible to confuse isolated pygidia of this species with *oklahomae* if the terminal spine is present, and with *huntonensis* if it is absent. The finer ornament, the presence of granules on both anterior and posterior pleural bands, the less sharply upturned postaxial ridge, and the different proportions of the doublure all permit



Text-figure 27. Ventral and lateral views of reconstructed enrolled specimen of *H. (Huntonia) lingulifer* (Ulrich and Delo).

lingulifer to be distinguished from *oklahomae*. The differing number of rings and pleurae, the less abrupt terminus on the axis, the upturned postaxial ridge, and the different proportions of the doublure enable it to be distinguished from *huntonensis*. It will be noted that the end of the axis, and the postaxial morphology and doublure, as well as the ornament, are vital in making these distinctions. Terminally broken and slightly worn specimens are therefore often difficult to place.

The narrow upturned anterior process and the uniform ornament make the cephalon easy to distinguish from other species.

There are no described species outside the Haragan fauna with which *lingulifer* is likely to be confused.

Material.—Haragan Formation: OU 3428, 6566, 6570, 6574, 6576, 6588, 6589, 6591, 6599, 7209; several specimens labelled USNM 483d and USNM 79031; ANU 14847, 21028; all from Hunton Townsite, NW¼ sec. 8, T. 1 S., R. 8 E., Coal County. OU 6590 from White Mound, SE¼NE¼ sec. 20, T. 2 S., R. 3 E., Murray County. Several specimens labelled USNM 79031 from west side of NW¼ sec. 21, T. 1 S., R. 8 E., Coal County. OU 3430, 6603 from NW¼ sec. 33, T. 1 S., R. 8 E., Coal County, Amsden collecting locality C2.

Bois d'Arc Formation: OU 3640 and 5379A-F from small quarry near highway 18, SW¼ sec. 36, T. 1 S., R. 3 E., Murray County.

Huntonia (Huntonia) oklahomae

(Richardson, 1949)

Pl. 19, fig. 6; pl. 23, figs. 1-6; pl. 40, fig. 4

Dalmanites oklahomae RICHARDSON, 1949, p. 43-45, text-figs. 14-15.

Dalmanites oklahomae Richardson; AMSDEN, 1956, p. 34.

Types.—Holotype, Chicago Natural History Museum P10435, from the Haragan Formation at Bromide, Coal County, Oklahoma (see Amsden, 1956, for a discussion of the locality and its stratigraphic position).

Diagnosis.—Cephalon is similar to that of *H. (Huntonia) lingulifer* (Ulrich and Delo) except for the following features: length of anterior lobe 0.65-0.68 times its width; eyes with 40-42 files with a maximum of 10 lenses per file; more obtuse genal spines; coarser glabellar ornament around its outer parts, tending to be smooth medially; also coarser ornament on the lateral parts of the fixed cheeks. Thorax is without ornament on the axis or the pleural bands, or with a few scattered granules like those on the glabella on the lateral parts of the axis and anterior bands. Pygidium has similar proportions to *H. (Huntonia) lingulifer* but is less contracted at the base of the caudal spine, which is at least four-fifths the length of the pygidial axis; ornament is coarsest on the flanks of the axial rings, finer on the anterior pleural bands, and finest on the border; posterior pleural bands are unornamented or bear a few small granules.

Description.—Four specimens with cephalon, thorax, and pygidium associated are available, and they vary in pygidial width from about 20 mm to 48 mm, thus covering a large part of the holaspid range. Of these, the largest pygidium is incomplete, but it would not have been more than 50 mm wide. Over this growth range the characters listed in the diagnosis are constant. This holds for the eye counts as well as for other characters.

The subocular platform is widest at its anterior end and in front of the posterior limb of the suture, but in between it thins out to about half that width. The anterior cephalic process is well preserved on two individuals, and on one of these it is asymmetrical. The extremity is slightly bilobed. The length of the process measured from the preglabellar furrow is 0.4 times the length of the glabella. The preglabellar furrow is only faintly developed, usually being represented by little more than a discontinuity in the ornament. The anterior limb of the facial suture lies parallel to this furrow and about 0.25 mm outside it, except medially, where the suture swings farther forward to form a pronounced lobe on the base of the anterior process. The genal spines are robust and extend back to the level of the fifth thoracic axial ring. The eyes stand high above the glabella. In lateral profile the posterior edge of the visual surface is slightly convex and almost vertical, whereas the anterior edge is also convex but is inclined at about 60° to the horizontal.

The cephalic ornament is most distinctive. The granules on the glabella, on the anterior cephalic process, and in the angle between the lateral and posterior border furrows on the fixed cheek are coarser than elsewhere. On the larger specimens they are 4-10 per square mm. They are also coarse around the subocular platform, the top of which, however, is smooth. Below this platform the granules become finer and sparser. On the lateral borders the granules are fine but are graded in size with the finest ones around the margin. There are a few coarse granules on the palpebral lobe and a few more on the anterior end of the palpebral rim, which is otherwise smooth. The posterior border is smooth or has a few large granules proximally. The axial part of the glabella and the whole occipital ring appear to be smooth, or they may have an occasional large granule.

The cephalic doublure is narrow and at its widest part is only one-third the width of the occipital ring.

There is one specimen of a hypostome in position beneath a fragmentary cranidium, which, from the ornament and eye morphology, must belong to this species. The outline tapers strongly toward the rear, where it is only 4 mm wide as compared with a width of 27 mm across the anterior wings. There are three pairs of lateral spines and a terminal one. A line joining the anterior pair of spines passes just in front of the maculae, and a line joining the median pair passes just in front of the extremity of the posterior border furrow. The surface has been extensively abraded, but the granulation preserved is much finer than that of the associated glabella; from other material, I estimate that it was finer than that on the associated lateral cephalic borders. It is slightly coarser on the anterior rim of the hypostome than on its lateral borders and median body. The whole surface of the median body is covered with pits, probably representing areas of muscle insertion.

The thoracic segments have the normal shape for the genus, but their ornament is most distinctive. On the smaller specimens the axial rings are smooth except for a few granules on the posterolateral edges the same size as those on the glabella; the anterior and posterior bands have a few scattered granules of the same size along their crests and more concentrated smaller granules along the back of the pleural facet. On the larger specimens the rings and the posterior bands seem to be completely smooth, and the anterior bands are smooth or carry very scattered granules proximally and denser ones on the distal extremity behind the facet.

The pygidium is a standard Type B and has 13 or 14 complete and 1 incomplete ring plus a terminus, regardless of size. There are invariably 12 pleural furrows, the last being extremely faint and situated well up on the flanks of the postaxial ridge. The axis is poorly defined posteriorly, and the postaxial region is a broad triangle in section, with a bluntly rounded crest. A short distance behind the axis it turns up into the spine, the crest of which lies at about 30° to the horizontal. The only spines available are incomplete. Measured from the end of the axis, the longest one is about four-fifths the axial length, and I estimate that it would have been as long as the axis before breakage. The margin is not pinched in at the base of the spine but continues back some distance beneath it, giving the whole structure a characteristic shape. The axial rings carry numerous granules of similar size to those on the glabella on their lateral parts, with finer granules on the axis. The anterior pleural bands have finer granules that become progressively finer and more closely spaced toward the densely granulated border. The posterior bands are either smooth or carry a single row of scattered granules along the crest. The doublure has a pronounced arch for the reception of the anterior cephalic process.

Remarks.—The four associated specimens are sufficiently well preserved to permit the ready identification of isolated cephala and pygidia. In addition, the ornament on the glabella and the axial region of the pygidium is so similar that isolated parts can be readily recognized. Neither is there doubt that they belong to *oklahomae*, although the type specimen is quite fragmentary. Through the courtesy of Dr. Matthew Nitecki, I have been able to examine a cast of this specimen. It has 40 or possibly 41 files of lenses, with a maximum of 10 per file; the eye morphology is identical with that of the specimens described above. Similarly, the overall ornament and the proportions of the glabella and palpebral lobes are identical. The base of the anterior cephalic process is of comparable shape and dimensions, as is the doublure.

The amount of variation in the sample is small. There may be some slight variation in the shape of the anterior process and the length of the genal spines, but there is not enough material to be sure of this.

Richardson (1949, p. 45) made several comparisons with species that had been reported from the Hunton Group by Reeds (1911), but none of the species listed is closely comparable to *oklahomae*. The only form with which it is likely to be confused is *H. (H.) lingulifer*, which has a similar overall shape, anterior cephalic process, and long upswept terminal spine. Both these species occur at the type locality of *oklahomae* and at the Old Hunton Townsite locality. This might lead to the conclusion that the described forms represent the two ends of a continuously varying series, but this is definitely not so; no intermediates have been found. Neither is it possible that the two represent small and large individuals of the one form. Although *oklahomae* is generally larger than *lingulifer*, the overlap in size between the two populations is great, and specimens of comparable size are readily distinguishable using the features listed in the diagnosis.

Other material.—OU 3410, 3427, 6565, 6568, 6575, 6596, 6597, 6600, 6604, 6606; ANU 14247, 14690; USNM 483d(7), 483d(8); all from various levels at Old Hunton Townsite, NW¼ sec. 8, T. 1 S., R. 8 E., Coal County.

Huntonia (Huntonia) huntonensis

(Ulrich and Delo, 1940)

Pl. 21, figs. 1-5; pl. 22, figs. 1-5

Dalmanites huntonensis Ulrich and Delo; Delo, 1940, p. 42, pl. 3, figs. 26, 28.

Dalmanites huntonensis Ulrich and Delo; Amsden, 1956, p. 46.

Types.—Holotype USNM 79036, from the Atoka quadrangle; specimen figured by Delo (1940, pl. 3, fig. 26). In the text, this specimen and the one figured in figure 28 of the same plate (now labelled USNM 111572) are said to be cotypes, but the plate explanation nominates them as holotype and paratype, respectively. Under the same number is a cranidium that bears the label "unfigured paratype." This specimen belongs to *Huntonia (Huntonia)*, new form, described below.

Diagnosis.—Cephalic profile is depressed; glabella expands gradually, with the occipital ring 0.65-0.70 times the width of the anterior lobe; length of anterior lobe measures 0.70-0.8) times its width; anterior lobe is depressed and is bordered anteriorly and laterally by a shallow dorsal furrow, outside which the facial suture lies at a distance of about 1 mm on the largest specimens, except in front where it sometimes swings onto the base of the anterior process; anterior process approximately equals width of the occipital ring proximally, is triangular in outline but contracts abruptly about halfway along its length; ventral surface of process is gently convex to flat and in lateral profile is only slightly upturned toward its tip; the eye has 42 files of lenses with a maximum of 10 in any file; subocular platform is wide anterolaterally, decreasing abruptly in width front and back; epi-border furrow is distinct, broad, and shallow; genal spine is long and low, extending back to the 7th or 8th thoracic ring, the terminal angle being about 10°; outer part of cephalic doublure is broad and flat, and inner part high and vertical; greatest doublure width is reached anterolaterally, where it becomes half the width of the occipital ring; whole dorsal surface of cephalon is covered with fine granules that are slightly coarser on the glabella and inner cheeks than elsewhere; glabella also has scattered, slightly enlarged, perforated granules, varying in density, but commonest on the anterior lobe and lateral glabellar lobes.

Thorax is of normal shape for the genus; ornament is of similar type to that of cephalon, covering the whole surface, but enlarged perforated granules are often present on lateral parts of rings.

Pygidium is peltate in outline; axis has 15 complete and 1 incomplete rings plus terminus; 12-13 pleural furrows are visible, the last pair lying between the postaxial ridge and a very short rib; terminus of axis is sharply defined; postaxial ridge is broadly triangular with a blunt crest; terminal spine is variably triangular in outline, short, and lies almost horizontal; border is narrow; pleurae extend well outside the inner edge of the doublure and become slightly thickened where they cross it; doublure is wide, its maximum width being 0.40-0.45 times the width of the first axial ring; outer part of doublure is inclined at 15°-30° to the horizontal and curves upward only slightly at the posterior extremity; inner part of doublure is inclined at 30°-45° to the outer part, never vertical; whole dorsal surface is covered with fine granules except on the lateral parts of the axial rings, where they are 2 to 3 times coarser.

Description.—Seven specimens, showing parts of the cephalon, thorax and pygidium associated, are available. Some of these are far from complete, and all except two are only about half the maximum size. There is no associated specimen showing a complete pygidium, or even a pygidial spine in place. The largest cephalon is about 55 mm wide, and the largest pygidium is 53 mm wide.

The anterior cephalic process is not complete on any specimen, but its base is always approximately equal to the width of the occipital ring. On two specimens its proximal outline is almost parallel sided, and then there is a sudden decrease in width. On the other specimen it tapers more uniformly throughout. The anterior border is always strongly contracted at the base of the process. The subocular platform is sharp edged and is up to 1.5 mm wide on the largest specimens. At its anterior end it abruptly attains its maximum size lateral to γ and maintains this width to a point opposite δ, where it tapers abruptly. The preglabellar furrow is well defined all round, but it does not interrupt the surface ornament anteriorly. Laterally and anterolaterally, the facial suture follows parallel but well outside the furrow. There is a wide range of variation in the extent to which the suture swings forward onto the anterior process. The eyes are poorly known. Counts of 42 files were obtained on 2 specimens, and another eye 7 mm long has a maximum of 10 lenses per file. The cephalic doublure shows a characteristic widening opposite the end of the hypostomal suture, where it is proportionately wider than in any other species. The antennal furrow is strong.

The glabellar ornament consists of a groundmass of more or less uniform granules. Scattered between them are larger granules, from 0.20-0.30 mm in diameter, that exhibit a clear perforation. These vary greatly in number from specimen to specimen and are usually most concentrated on the anterior lobe and the lateral parts of the other glabellar lobes. They are rare on the occipital ring. The palpebral lobes and postocular part of the cheeks and posterior border have granules like the nonperforated ones on the glabella. Away from these areas, the ornament becomes progressively finer. The palpebral rim has finer and more closely packed granules than those on the palpebral lobe.

An inverted hypostome is present beneath one of the largest specimens. This hypostome has the typical outline and spine number of the subgenus and is 17 mm wide across the anterior wings and 6 mm across the posterior spines. A line joining the anterior spines passes well in front of the maculae, and another line joining the median pair passes well in front of the posterior extremity of the posterior border furrow. The ornament consists of a uniform cover of dense, fine (0.1-mm-diameter) granules, finer than those on the associated glabella.

There is little about the thorax that is distinctive. Granules cover the whole dorsal surface; they are a little coarser on the lateral than on the median parts of the rings. On the pleural bands, except on the distal extremities, they are finer than on the rings.

There are about 20 isolated pygidia available. They are of typical Type A form and show a range of variation in outline, particularly in the width of the specimen across the end of the axis and in the shape of the terminal spine. This was well shown by the two specimens figured by Delo. The figured paratype is wider behind the axis and has a much narrower based spine than the holotype. There is continuous variation in these features in the collection. The spine always extends almost horizontally. The axis also varies a little in the acuteness of its termination; in general, the smaller specimens are more acute. On some of the larger specimens, 13 pleural furrows can be distinguished, but on the smaller ones only 12 can be seen. The 13th furrow is very small, and the rib separating it from the neighboring furrow is only 1 mm or so long and is restricted to the slope of the postaxial ridge; the next to the last rib is also very short, but despite this, well-preserved specimens still show a faint trace of the interpleural furrow. The doublure is wide. Its inner part makes an angular junction with the outer part laterally, but toward the posterior this junction becomes less well defined, so that at the extremity the two parts form an even flat curve in profile. The ornament of the axis is differentiated more than that of the thorax into coarse granules laterally and finer ones medially, with some of the lateral granules clearly perforate. The pleural bands are finely ornamented, granules on the posterior bands being a little coarser (up to 0.20 mm in diameter) than those on the anterior bands; well-preserved specimens show the pleural furrows covered with a mat of even finer granules no more than 0.1 mm in diameter.

Remarks.—The most distinctive features of this species from the point of view of ease of recognition are the relatively broad anterior process with the flattened ventral surface, the narrow anterior glabellar lobe, the wide subocular platform, the glabellar ornament, and the wide cephalic and pygidial doublures. These features make it one of the easiest members of the subgenus to recognize even in a fragmentary state. The main difficulty arises with isolated pygidia, which show a wide range of variation in outline, inclination of the doublure, shape of the terminal spine, and overall convexity. Some of the variation in convexity may be due to distortion, and this could also explain some of the variation in the attitude of the outer part of the doublure. However, all four specimens with the pygidia joined to cephala and thoraxes show the inner and outer parts of the doublure undifferentiated posteriorly, and hence I have used this as a diagnostic pygidial character.

Delo commented that the "Posterior branch of each rib ends at the inner edge of the very broad doublure." The interpleural furrows certainly weaken as they cross the inner edge of the doublure, but they do continue out onto the border, where they separate a very weak posterior pleural band (*not* rib band, as stated by Delo) from the inflated anterior band of the next segment. He also listed the furrowed ribs as diagnostic. This feature is overrated, as these interpleural furrows are found on all the species I have examined, provided the surface is well enough preserved.

Similarity between this species and *Dalmanites carlwegi* Tansey from the Helderbergian Bailey Limestone of Missouri was noted by Delo (1940). The numbers of rings and pleurae he quotes for *carlwegi* are not correct, the figure of the holotype showing 13 or 14 rings and a terminus, and 13 pleural furrows, the last one being quite short. Thus, this species may be more closely related to *huntonensis* than Delo believed, though this cannot be checked without knowledge of the cephalon and details of the pygidial ornament.

Material.—Haragan Formation: OU 3410, 6567, 6572, 6580, 6581, 6582, 6584, 6586, 6604, two specimens labelled USNM 79035 and several specimens labelled USNM 483d; all from Old Hunton Townsite, NW¼ sec. 8, T. 1, S., R. 8 E., Pontotoc County. OU 5242, 6579, 6601; all from White Mound Area, sec. 20, T. 2 S., R. 3 E., Murray County. OU 6605 from NW¼ sec. 22, T. 2 N., R. 7 E., Pontotoc County.

Bois d'Arc Formation, *Cravatt Member*: OU 7200, Coal Creek, NW¼ sec. 22, T. 1 N., R. 7 E., Pontotoc County, Amsden collecting locality P9, M & N.

Huntonia (Huntonia) purduei purduei
(Dunbar, 1919)

Pl. 19, Fig. 7; Pl. 24, Figs. 1-7; pl. 25, figs. 1-5; pl. 30, figs. 2, 3

Dalmanites purduei DUNBAR, 1919, p. 54.
Dalmanites purduei DUNBAR, 1920, p. 148, pl. 5, figs. 1, 2.
Odontochile purduei (Dunbar); DELO, 1940, p. 62-3, pl. 6, fig. 1.
?*Odontochile acuminatus* Ulrich and Delo; DELO, 1940, p. 55, pl. 5, figs. 9, 10.

Diagnosis.—Cephalon is moderately convex; occipital ring of glabella measures 0.55-0.60 times the width of the anterior lobe; length of anterior lobe is approximately 0.65 times its width; anterior lobe is rather depressed in profile and is bordered by a shallow furrow lying inside of and parallel to the facial suture; anterior process of cephalon is wide, short, flat to slightly concave on the dorsal surface, moderately convex on the ventral surface, and rounded to bluntly angular in front; there is only a slight constriction in anterior border at base of process; subocular platform is wide anterolaterally; eye has approximately 42 lens files with a maximum of 11-12 lenses per file; genal spine is long and slender, probably extending back to the 6th or 7th thoracic segment; cephalic doublure is flat on its outer part and strongly upturned in its inner rim; hypostome is rather flattened, with 1 pair of lateral spines opposite the maculae, 2d pair opposite the extremity of the posterior border furrow, and a 3d on either side of the short median posterior spine. Thoracic segments have strong anterior band and pleural furrow but weak posterior band. Pygidium is trimorphic. Type A has 19 complete and 1 or 2 incomplete rings plus a terminus; 16 or 17 pleural furrows; border is of moderate width and is inclined at approximately 20° to the horizontal; maximum width of doublure equals maximum width of axial terminus; doublure has an almost horizontal outer band and a vertical inner rim; postaxial ridge is depressed, rounded on top, and extended into a short terminal spine that is ovate (but slightly flattened on the base) in cross section, and directed upward at only a slight angle to the horizontal. Type B has 17 or 18 complete and 1 or 2 incomplete rings plus terminus; 15 pleural furrows; border is narrow and steeply inclined; axis is poorly defined posteriorly, extends back into a well-rounded postaxial ridge, and has a long upswept terminal spine; outer band of doublure is narrow and moderately inclined, with inner rim vertical. Type C has 17 complete and 2 incomplete rings plus terminus; 15 or possibly 16 pleural furrows; axis is narrow, and defined posteriorly; postaxial region is broadly rounded; terminal spine is elongate, sharp, almost circular in cross section; doublure is narrow, never equalling the width of the axis.

Description.—Two specimens showing incomplete anterior cephalic processes are available, but from these pieces it is clear that they are of precisely the same shape as those on the Haragan material described below. The eyes are rather more asymmetrical than is normal for the genus in that ϵ is set farther out from the dorsal furrow. The lines joining γ-ϵ on each side of the glabella converge forward at about 20°, whereas in other species they are almost parallel. This position of ϵ also means that the posterior limb of the facial suture does not cut in quite so close to the eye, and therefore the subocular platform extends farther around behind the eye than is normal. The molds of the genal spines available are incomplete, but they show the posterior border furrow, the lateral border furrow, and the epi-border furrow in the characteristic relationships for the subfamily. The genal spines stand steep and are high, but they have a very narrow ventral surface and consequently appear to be quite slender in vertical aspect. Although it varies with specimen size, the granulation is fine and is more or less uniform over the whole cephalon. On an anterior glabellar lobe 20 mm wide there are 25-35 granules per square mm.

The hypostome is normal for the genus. The only specimens available, 1 complete and 2 incomplete internal molds, show precisely similar characters. The anterior border is shortest medially and increases slightly toward the wings. The posterior border furrow has a pair of depressions, one behind each macula, that show up strongly on the internal mold. The highest part of the posterior wings is situated a little behind the maculae, and the posterior doublure extends less than halfway from the posterior extremity to the posterior border furrow.

There are several molds of thoracic segments that show the standard dalmanitinid form on both surfaces. Their ornament is identical to that of the cephalon.

There is little to add to the information on the pygidia given in the diagnosis. The ornament on the dorsal surfaces of all three types is comparable.

Comment.—The above diagnosis and description are based on material from the type region and formation but not from the type locality. Not all the characters can be determined with certainty; for example, there are no complete genal spines, but enough is known to make a confident identification possible.

Dunbar's reconstruction of the cephalon is apparently inaccurate at many points. It has the anterior process too small, the glabellar outline too constricted posteriorly, the facial suture too broadly rounded at β and its posterior limb insufficiently flexed, the eyes too small, and the arrangement of the lateral and posterior border furrows incorrect. The genal spines are probably a little too short also. He commented that the pattern of the glabellar lobes indicates that the species belongs to the synphoriinids, but this is clearly not the case, as can be seen from the analysis in the discussion on the Superfamily Dalmanitacea given above.

It is possible that the small anterior process is indicative of the presence of a second type of head that corresponds with the Type B or Type C pygidium. One of the difficulties with the present interpretation is that there are too few heads available to analyze the variation in the shape of the anterior process. There is always the possibility that the shape of the process varies little between morphs and that the Type B pygidium is adjusted to the process by placing the doublure against its extremity, the Type A pygidium against its median part, and the Type C in an intermediate position.

Haragan specimens.—The Haragan specimens assigned to this species are not as well preserved as those from the type area. The pygidia are almost always broken, particularly at the posterior end, and the surface ornament is frequently removed. The size range is great, one pygidium being larger than all those from Pickwick Dam, but it is quite incomplete. There is an eroded individual, OU 8293, with thorax and pygidium giving an excellent idea of the high convexity of the animal. Finally, there are 3 broken cephala, all of which have part of the anterior process, 2 of which have the glabella and cheeks, and 1 has a genal spine.

The assignment of these specimens to *purduei* is not without some doubt. Although most of the pygidia fall readily into the 3 types of *purduei,* there is 1 large incomplete individual, OU 8292D, on which it is possible to count 21 rings and 17 furrows, and there could be 1 or 2 more of each. This would make them more numerous than in *purduei.* Also, there are no individuals showing the complete postaxial characters of Type A or Type C. However, the similarities between the collections in all other characters, except perhaps the eyes (see below), are so great that it would be impossible to differentiate them. Delo (1940, p. 55) referred forms of this type to *O. acuminatus,* which is discussed below.

The two cephala are well preserved, and OU 6573 is larger than the available Tennessee specimens. At the anterolateral corners of the glabella, the facial suture develops a slight angularity not seen on the smaller specimens. This individual also shows the areas of muscle insertion in the 3p furrows particularly well. The hypostomal suture is strongly concave backward, and its extremities lie directly beneath the widest parts of the anterior glabellar lobe. The anterior border is only slightly constricted at the base of the anterior cephalic process. On each flank of this process there is a slight swelling, so that its outline is similar to, but more subdued than, that of *H. (H.) huntonensis*. The muscle insertions into the anterior lobe of the glabella are well shown, and these are closely comparable with those in *purduei fittstownensis*. The anterior lobe at its anterior extremity has the appearance of being slightly crumpled, presumably because of the insertion of large muscles there. Behind that there are 6 to 8 highly irregular rows of scars that radiate from the posteromedial part of the lobe toward the front. The strongest ones are situated in the fronto-median part of the lobe. The larger specimens also shows particularly well the collars around the perforations associated with the granulose ornament, and this same specimen has the eyes rather well preserved. There are 46 files of lenses, with a maximum of 12 per file. This is to be compared with numbers of 42 and 11, respectively, in the Tennessee specimens, but the Haragan eye is 1.5 times longer. Unfortunately, only one specimen at each locality is well enough preserved to permit the lenses to be counted, and consequently no secure conclusions can be drawn from these data.

The single Haragan specimen showing the thorax has nine segments attached to a Type A pygidium, but the whole individual is badly eroded, and the surface is not preserved anywhere. It is of interest in that it is undistorted and shows the high convexity of the thorax and the abrupt expansion of the width of the rings on the thorax. The following are the dimensional details (in mm):

Width of pygidium	Width of axis of pygidium	Maximum width of thoracic axis	Maximum height of whole thorax
57	16	22	16

Bois d'Arc specimens.—These specimens are all fragmentary and distorted, but in most observable characters they are comparable with the Haragan specimens. It is possible that in the postaxial region of the Type B pygidium they are more like *H. (Huntonia) lindenensis* than *H. (Huntonia) purduei*.

Remarks.—There are several Early Devonian species to which *H. (Huntonia) purduei* can be seen to be related, despite the fact that little is yet known about them. These include *H. (Huntonia) acuminata* (Ulrich and Delo), from the "Helderbergian" limestone, Tishomingo County, Mississippi; *H. (Huntonia) dunbari* (Delo), from the Bailey Limestone, Ste. Genevieve County, Missouri; and *H. (Huntonia) mississippiensis* (Delo), from the "Helderbergian" of Mississippi. The first three of these species were assigned to *Odontochile* and the last to *Dalmanites* by Delo (1940).

In my opinion, the features that unite this group are the number of pygidial rings and pleurae, the depressed surface of the lateral parts of the axial rings, the shape of the pleural bands, and the regularity of the ornament. In the case of *purduei* and *lindenensis*, for which cephala are known and a number of pygidia are available, additional unifying features are the shape of the anterior cephalic process, the position of the eyes, the depressed anterior lobe of the glabella, a uniformly fine granulation of the cephalon, and dimorphism or trimorphism of the pygidia.

Several specimens of *lindenensis* from Swaynes Mill, Big Sandy River, Tennessee, labeled 79050 and 163977 in the U.S. National Museum, have been examined, and two cephalic fragments are figured herein (pl. 29, figs. 4, 5). The main distinguishing features of *lindenensis* and *purduei* are that the former has (1) a less convex ventral surface on its anterior cephalic process, which becomes proportionately much shorter with increasing specimen size; (2) extremely fine granulation between the normal granules of the cephalon; (3) slightly more scattered granules on the lateral parts of the pygidial axial rings and more concentrated granules on the median parts; and (4) more scattered granules on the pygidial pleurae. Some of the slightly larger granules on the axis of *lindenensis* are obviously perforated, a feature not seen in *purduei*, though fine perforations are probably present. It should be noted that the type specimen figured by Delo (1940, pl. 4, fig. 26) is a young specimen and that the number of rings is more likely to be 19 or 20 plus a terminus than the 16 or 17 reported by Delo, and the number of pleural furrows is 16 rather than 14 or 15.

Odontochile acuminatus Ulrich and Delo was based on the internal mold of a pygidium of Type C. It has 19 complete and 1 or 2 incomplete rings plus a terminus, and 16 or possibly 17 pleural furrows. Doublure and terminal spine are of standard Type C form. Through the courtesy of Dr. F. Collier of the Smithsonian Institution, I have been able to examine the holotype specimen (pl. 30, fig. 1). Preservation is in the form of molds, but part of the skeleton of some specimens has been replaced by silica. There are several other fragmentary specimens of the same species on the block, and from these the following information has been obtained. Beneath the holotype is a large, broad pygidium lacking the posterior end, but probably of Type A. The pygidial ornament is the same as in *purduei*. Most of a cranidium and the ventral surface of an anterior cephalic process are preserved separately. Form and ornament are precisely the same as those of *purduei*. A large part of a free cheek, including an eye, is preserved as an internal mold. The lenses have been partly replaced by silica and are described above. As far as I can determine, this species is not distinguishable from *purduei purduei*, although it must be emphasized that the genal regions, the hypostome, and the Type B pygidium have not been observed. For this reason, it is listed as a doubtful junior synonym.

According to Delo (1940, p. 56), only the pygidium of *H. (H.) dunbari* is known. He recognized only two specimens of Tansey's original collection (Tansey, 1922, pl. 55, figs. 2-7; pl. 56, fig. 1) as belonging to the species. Lespérance (1975), adopted the same stance, though he tentatively included the species in his new genus *Forillonaria*. It is not known if all Tansey's specimens came from the one locality, but from what is known of the variation in *purduei*, they could be regarded as members of the one species. The specimen on his plate 55, figure 6, could well be a small individual of one morph, and figure 5 an average individual of another morph. The two fragmentary glabellae figured have wide occipital regions, depressed and transverse anterior lobes, and figure 3, at least, has the facial suture outside the preglabellar furrow. All these are features of *purduei* and *lindenensis*. In addition, the glabellar furrows are of precisely the same kind as those of the Haragan specimens of *purduei* and give no reason for divorcing these specimens from the figured pygidia as was suggested by Lespérance (1975, p. 127). Finally, it is not impossible that the cephalon Tansey separated off as *Dalmanites* cf. *D. griffoni* Clarke also belongs to *dunbari*. This is of considerable importance, as it has an anterior cephalic process almost identical in size and shape to those of one of the Yale specimens of *H. (H.) lindenensis* and of a small individual of *H. (H.) purduei fittstownensis*. There is some confusion about the number of axial rings and pleurae of *dunbari*. Delo reported 18 rings and 12 distinct and 1 indistinct ribs. Lespérance counted 19 rings, concluded there could be more, and recorded 13 ribs. Although none of the specimens is complete, it is clear that Lespérance is correct about the ring count, and I estimate that the complete number in the holotype must be 20 plus a terminus; there must be at least 14 pleural furrows (and probably 15) on the holotype. The other figured specimens show similar numbers when allowance is made for incompleteness. This means that there is little left to separate *dunbari* from *purduei*. Delo contends that the axis of *dunbari* is wider, and that more interpleural furrows are present, but the shape of the axis of the holotype falls in the *purduei* range; and when external surfaces are compared there is no difference in the number of interpleural furrows. I suspect, therefore, that when the heads of *dunbari* are studied in detail the species may have to be placed in the synonymy of *purduei*.

I have examined only a cast of the holotype of *H. (H.) mississippiensis*, a partly exfoliated pygidium. It has the characteristic Type B outline, pleurae, and terminal spine, to judge from the small part of the doublure preserved. It must have had 20 axial rings plus a terminus, and there are at least 16 pleural furrows. Unless there are differences in the axial ornament, which is not preserved on the holotype, it would not be possible to distinguish this specimen from specimens of *purduei* of comparable size.

Material.—Ross Limestone: Ten pieces, none complete, labeled USNM 144308 and 94592, Pickwick Dam, Tennessee.

Haragan Formation: OU 6598, 8289-8291, 8291A, from northeast of Bromide, NW¼ sec. 33, T. 1 S., R. 8 E., Coal County, Amsden collecting locality C2. OU 8292A-D from west of Mill Creek, SE¼NW¼ sec. 12, T. 2 S., R. 4 E., Johnston County, Amsden collecting locality J11-D. OU 6573, 6602, and USNM 483d from Old Hunton Townsite, NW¼ sec. 8, T. 1 S., R. 8 E., Coal County, Amsden collecting locality C1. OU 8293, from north of Coal Creek, NW¼ sec. 22, T. 1 N., R. 7 E., Pontotoc County, Amsden collecting locality P9-K.

Bois d'Arc Formation: OU 5379g-m, quarry east of Highway 18, about 6 miles south of Sulphur, sec. 36, T. 1 S., R. 3 E., Murray County.

Huntonia (Huntonia) purduei fittstownensis, new subspecies

Pl. 26, figs. 1-7

Types.—Holotype, OU 7196A from the Fittstown Member, Bois d'Arc Formation, NE¼SW¼ sec. 35, T. 2 N., R. 6 E., Pontotoc County. Paratypes, OU 7196B, OU 7202-7, same unit and locality.

Diagnosis.—Differs from *purduei purduei* in the following: coarser ornament on the glabella; 17 or 18 complete and 1 or 2 incomplete rings plus terminus on the pygidium of both Type A and Type C; pygidial doublure of Type A that is as wide as the axis at the 16th ring; axis that stops farther from the border; in Type A, postaxial ridge and terminal spine that are more angular on the crest; shorter terminal spine; pygidial ornament that is coarser all over.

Remarks.—This subspecies also reaches a considerable size, the largest measurable pygidium available to me being about 90 mm wide and 65 mm long, excluding the terminal spine. There are fragments indicating that larger sizes were reached.

The morphology is still incompletely known, particularly that of the cephalic margins. The only piece of the free cheeks available is part of a doublure with an anterior cephalic process similar in size and shape to that of *purduei purduei.* Glabellar proportions, position and shape of the palpebral regions, and shapes of the various dorsal and glabellar furrows seem to be indistinguishable from those of the nominate subspecies.

The size of the glabellar granules varies considerably with the size of the individual and to a lesser extent with position on the glabella. In general, it is finest and densest on the lateral parts of the anterior lobe. On the largest specimens it tends to be effaced toward the midline, but this could be the result of abrasion. On the anterolateral parts of an anterior lobe 41 mm wide, the granules are 0.4-0.5 mm in diameter and number about 5 per square mm. In the same position on a lobe 25 mm wide, the figures are 0.2-0.3 and 15, respectively. The granules on the palpebral region and the postocular fixed cheeks are similar to those on the adjacent parts of the glabella.

The hypostome is represented by a single broken specimen. It is more elongate than that of *purduei purduei:* there is a slight bulge in the outline opposite the depression in the posterior border furrow; a line joining the opposed second lateral spines is situated behind the posterior border furrow; and the posterior tip is drawn out into a much longer triangular spine than that of *purduei purduei.* Some of these differences may be related to differences in size.

The pygidia of Type A and Type C are well represented and the external surfaces are better preserved than in the types of *purduei purduei.* Type B is represented by small individuals only. The numbers and shapes of the rings and pleurae are entirely comparable with those of *purduei purduei.* Type A has quite an angular postaxial ridge that extends out along the spine, which thus has a depressed triangular section rather than the dperessed ovate section of *purduei purduei.* The postaxial ridge is not so sharp on Type C, in which the axis terminates a little more abruptly and also farther forward than in the Type C of *purduei purduei.* The ornament on both types is finest on the border and becomes slightly coarser on the pleurae. It is slightly coarser still on the lateral parts of the rings but fines again to the axis.

Other Material.—Five specimens labeled OU 7208, from a calcarenite near the top of the Haragan Formation in Chimneyhill Creek, NW¼SW¼ sec. 4, T. 2 N., R. 6 E., Pontotoc County, Amsden collecting locality P1-U. All these are slightly worn, but their pygidial segmentation and their glabellar shape and ornament are almost identical with those of the Fittstown specimens.

Huntonia (Huntonia), new form

Pl. 27, figs. 1-5

Material.—All from the Haragan Formation. OU 3443, OU 6583, and USNM 208987 from Old Hunton Townsite; OU 6571 from north of Coal Creek, NW¼ sec. 22, T. 1 N., R. 7 E., Pontotoc County, Amsden collecting locality P9-K; OU 8275 from Northeast of Bromide, NW¼ sec. 33, T. 1 S., R. 8 E., Coal

County, Amsden collecting locality C2(1); OU 6564 from Vines Dome, NW¼NW¼ sec. 2, T. 2 S., R. 2 E., Murray County, Amsden collecting locality M1-K.

Diagnosis.—This form is moderate in size. Glabella has low anterior and lateral profiles; length of anterior lobe measures 0.6-0.7 times its width; preglabellar furrow is weak, and anterior lobe of glabella extends forward into a slight tongue; anterior process at its base is approximately equal in width to the occipital ring; length of anterior process is unknown; anterior border is strongly contracted at base of process; facial suture has an anterior swing matching the outline of the anterior glabellar lobe; eyes have 40 files, with a maximum of 11 lenses per file; subocular platform is narrow all round; border is narrow, with a shallow epi-border furrow; genal spines are short, extend back to the level of the 4th thoracic ring, and have a strong epi-border furrow; glabella is covered with granules that are slightly coarser and sparser on lobes 1p and 2p. Hypostome outline is strongly tapered; width across posterior measures about one-third of width across anterior (exclusive of wings); anterior outline between wings almost forms the arc of a circle of 12 mm radius; anterior wings are high and long; there are 3 pairs of tiny lateral spines, the 1st opposite the maculae, the 2d well in front of the posterior border furrow, and the 3d at the posterolateral extremity; surface is uniformly covered with fine granules. Thorax is normal for the genus; rings and both anterior and posterior pleural bands have granules like those of the glabella. Pygidium has 14-15 complete rings, 1 or 2 incomplete, and a terminus; axis is well defined posteriorly; blunt postaxial ridge extends into a narrow-based, sharp, horizontal terminal spine, equal to about one-third the length of the axis; spine is slightly keeled on top, rounded on the bottom; doublure has a wide flat outer part and a steep high inner part; outer part is horizontal except at posterior extremity, where it is slightly curved upward; ornament consists of granules on rings and pleurae, those on the rings being slightly the coarser.

Remarks.—This is the last securely based "species" of *Huntonia* described herein. The most complete specimen, OU 3443, has neither the glabella nor the pygidial terminus preserved, and the other specimens are isolated cephala and pygidia. It is impossible to be certain that they are members of the one species, though they do form a homogeneous group.

There is no point in assigning a new specific name to this group, because it is probably one of a dimorphic pair for which a name is already available. Which described form is its fellow cannot be decided at present. The specimens come from four localities, and no other "species" of *Huntonia* is known from all of them.. The pygidium is similar in many respects to the Type C, and the glabellar profile is flat like that of *purduei purduei,* but the possibility that it represents a Type C of that subspecies is discounted because of the shape of the base of the anterior cephalic process and the anterior border.

For the present, it is noted that the form may be distinguished from *huntonensis* by the shape of the glabella, the narrow cephalic doublure, the narrow ocular platform, and a more pointed pygidial spine; it is distinguished from *oklahomae* by its finer glabellar ornament, an ornamented rather than smooth thorax, and a short horizontal pygidial spine; and from *lingulifer* by its flatter glabellar profiles, its shorter genal spines, a more peltate pygidium, and a shorter horizontal pygidial spine. It is difficult to distinguish isolated cephala of this form from those of *H. (H.) oklahomae.*

Subgenus **Prosocephalus**, new subgenus

Type species.—Huntonia (Prosocephalus) xylabion, new species, from the Bois d'Arc Formation, Fittstown Member, Oklahoma.

Diagnosis.—Exoskeleton is of moderate size; glabella is narrow across lobes 1p, which are only a little more than half the width of the anterior lobe; eyes are large and surmount a narrow, flat subocular platform; ϵ on facial suture is situated opposite the occipital furrow, and eyes are so far back as to constrict the posterior border furrow; lateral border has a strong epi-border furrow; anterior process is short, broad, either trifid or quadrate, and has a deep embayment of the border at its base; genal spines are thick and long; doublure has flat outer and vertical inner portions; ornament on glabella consists of granules and in some specimens also of scattered small tubercles, and ornament elsewhere is of granules only.

Pygidium has low convexity; axis has 10 to 12 complete and 1 or 2 incomplete rings plus a terminus; 9 to 11 pleural furrows; postaxial ridge is rounded and is extended into a short, blunt spine semi-elliptically shaped in cross section; ornament is granulate.

Other species assigned.—Dalmania tridentifera Shumard, 1855, from the *Delthyris* shaly limestone (now the Bailey Limestone), Perry County, Missouri; *Dalmanites palaceus* Savage, 1913, from the Bailey Limestone of Illinois and Missouri; ?*Synphoroides biardi* Clarke of Haas, 1969, from the Solis Limestone of New Mexico.

Remarks.—This group is recognized primarily by the nature of the anterior cephalic process, but it is also distinguished by the posterior position of the eyes and the small pygidium with relatively few rings and pleurae. There is insufficient material for a study of dimorphism to be prepared, and it may be that the shape of the pygidial spine that is listed as diagnostic of the genus is characteristic of only one morph.

During enrollment the pygidial doublure rested against the anterior extremity of the cephalic process, so that water could gain access to the limbs through embayments both at the base of the process and at its end. In the case of *H. (P.) palacea,* it is probable that there was an open area at the end of the process, as shown in text-figure 22b. It is this overlap of the anterior cephalic spine by the posterior end of the pygidium to produce several openings that is regarded as the main means of distinguishing this subgenus from *H. (Neoprobolium)* and *H. (Huntonia).*

The members of the group may be confused with various synphoriinids that also have modified anterior borders. For example, the specimens from the Solis Limestone (Siegenian) figured as *Synphoroides biardi* Clarke by Haas (1969) probably belong to this genus. They have no accessory lobes lateral to the main trifid anterior process, as is normal for *S. biardi;* there is a slight constriction of the border at the base of the process, which is not found in *S. biardi;* the genal spines are unusually long for that species, or even for that genus; there is a distinct epi-border furrow, which is not a feature of the synphoriinids; and the shape of the pleurae and terminal spine on the pygidium are indicative of dalmanitinid rather than synphoriinid affinities. Most of these features suggest that the species is a member of *H. (Prosocephalus),* but without the posterior part of the glabella it is impossible to be certain of this. If it does belong to that subgenus it cannot be assigned to *H. (P.) tridentifera,* because of the shapes of its genal spines and its anterior cephalic process. The latter feature also excludes it from *H. (P.) xylabion.*

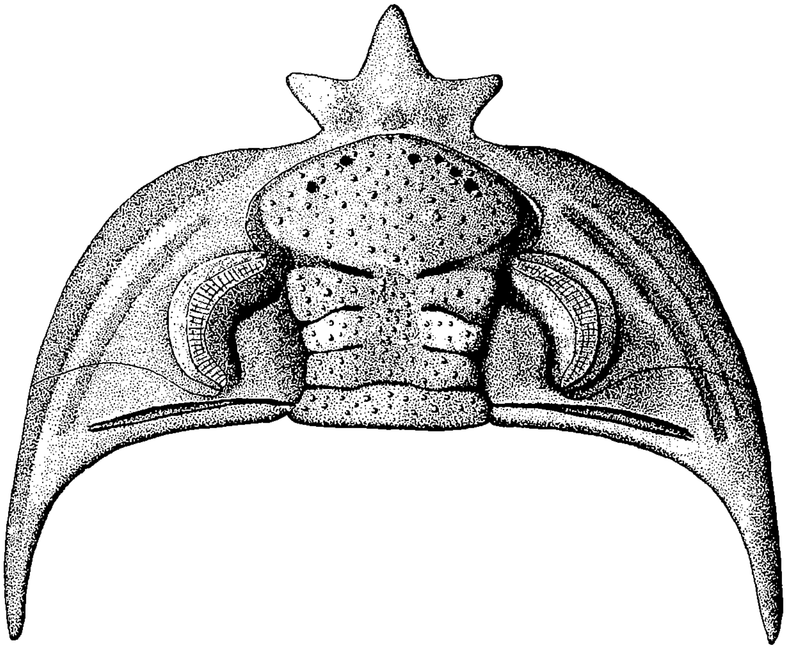
Huntonia (Prosocephalus) xylabion
new species
Pl. 28, figs. 2-4

Types.—Holotype: OU 6546 from the Bois d'Arc Formation, Fittstown Member, at Bois d'Arc Creek, SW¼NE¼ sec. 11, T. 2 N., R. 6 E., Pontotoc County, Amsden collecting locality P11-A. Paratypes: OU 6542-3 from the Fittstown Member at Henryhouse Creek, SE¼ sec. 30, T. 2 S., R. 1 E., Carter County, Amsden collecting locality Ca1(2)-V(2); OU 6244 from the Fittstown Member at Old Hunton Townsite NW¼ sec. 8, T. 1 S., R. 8 E., Coal County, Amsden collecting locality C1-Q. OU 6245a-b from the Fittstown Member west of Mill Creek, SE¼NW¼ sec. 12, T. 2 S., R. 4 E., Johnston County, Amsden collecting locality J11-L.

Diagnosis.—Anterior cephalic process is short, trifid, with angular extremities; glabella is sparsely tuberculate, with fine granules present between the tubercles, at least on the anterior lobe; lateral parts of lobes 2p and 3p are raised above the median parts; facial suture has angular bends both in front of and behind β; pygidium has length/width ratio approximately 6/7; there are 12 complete rings and 1 or 2 incomplete ones plus a terminus; 10-11 pleural furrows are present; border has slight traces of pleurae; pygidial ornament consists of granules only.

Description.—Cephalon is transverse; length (sag. including anterior process) measures three-fifths width (estimated); maximum width of glabella measures approximately three-fourths its length; glabella is widest at occipital ring, narrows to furrow 1p, expands again to the middle of lobe 3p, where the width equals that of the occipital ring, then there is a more gradual expansion to the anterior edge of furrow 3p, and finally an even more abrupt expansion around the anterior lobe; maximum glabellar width occurs at two-thirds the length of anterior lobe; occipital ring is not well preserved but is approximately twice as long medially as laterally; occipital furrow becomes weak medially; furrow 1p is pronounced, is directed obliquely backward, and joins with the axial furrow; furrow 3p is short (exsag.) axially, expands laterally to a maximum just inside the axial furrow, then contracts slightly; central part of glabella between lobes 2p and 3p is slightly depressed, but no defined longitudinal furrows are present; lobe 2p is slightly higher than anterior lobe. Palpebral lobes and eyes are not preserved; facial suture shows ω on a line joining the abaxial ends of furrow 1p and ϵ almost at the edge of the posterior border furrow; γ is almost on the edge of the axial furrow, just in front of the midlength of lobe 3p; anterior part of suture has a peculiar polygonal shape well shown on pl. 28, fig. 4b; on anterolateral flanks of anterior lobe, each branch of suture is concave forward and lies just outside the shallow preglabellar furrow. The subocular platform is narrow and is almost horizontal (about 1 mm wide) around base of eye, and its outer face is steep but rounded; cheek below platform is steep, narrow, and convex; lateral border furrow is broad and shallow; a broad, subangular crest on inner part of border fades away rather abruptly near the glabella; epi-border furrow is distinct; border is nipped in at base of anterior process, which is strongly trifid; surface of process is gently convex but has a faint ovate depression on either side of the midline near its base; genal regions are not preserved. Ornament on glabellar lobes and median depressed area of glabella consists of irregularly scattered, low tubercles ranging in diameter from 0.2-0.6 mm; there are 6 or 7 tubercles on the anterior border, forming a row along the inner edge of the facial suture; 10-12 irregular pits form an open V on the anterior slope of the glabella; border and anterior process have fine granules; cheek below ocular platform has low, irregular ridges, probably of caecal origin, and granules. Doublure of free cheeks is flatly convex toward the margin but has a steep inner portion, its edge lying against the border inside the epi-border furrow.

Pygidium is subtriangular in outline; length (sag.)/width ratio is about 6/7; profile is rather flat; axis tapers evenly except at



Text-figure 28. Reconstructed cephalon (*a*) and pygidium (*b*) of *H. (Prosocephalus) xylabion,* new species. Genal spines are not preserved and have been interpreted in terms of spines of *H. (P.) tridentifera* (Shumard).

the tip, where it is slightly expanded and well rounded; axis is flatly rounded in section, terminating anterior to the inner edge of the doublure; there are about 12 clearly defined axial rings, and 1 or 2 incomplete ones, plus the terminus; rings are flat in lateral profile and are more or less completely transverse; posterior edges of anterior 9 rings have distinct pseudo-half rings; apodemal pits are narrow, straight, and slitlike, but the furrows become shallow medially; 10 or 11 pleural furrows can be seen, the most posterior 2 almost indistinguishable and directed almost straight backward; pleurae are separated by distinct but fine interpleural furrows that can be distinguished on all but the last few ribs; pleural furrows are a little less than half the length (exsag.) of the pleurae; anterior and posterior pleural bands swell slightly as they approach the border, forming a distinct but low "rim" and then fade abruptly on to the border; outer part of border is smooth; posterior spine is short, subtriangular to subrounded in cross section, flat on the base, and slightly upturned toward its tip. Ornament consists of coarse granules on the axial rings; border and spine have dense fine granules; more scattered fine granules are present on the pleurae. Doublure has a flatly convex outer part and a steep inner part, its inner edge lying adaxially of the "rim" on the dorsal surface; surface is granulate, with the coarsest granules at the margin and progressively finer ones inward; vertical part is smooth.

Remarks.—This species is known from one incomplete cephalon and several almost complete pygidia. The cephalon is from a different locality from the pygidia, and hence there must be some doubt about the association. Nevertheless, I am confident the cephalon and pygidia are correctly associated, for the following reasons: There are three types of cephalon and three types of pygidium in the Fittstown Member. Those belonging to *H. (H.) purduei fittstownsensis* are easily recognized because of their large size, their abundance, and their occurrence at the same localities. The 1 head and 1 of the 2 tails assigned to *Odontochile syncrama* occur together, and this leaves the head and tails assigned to *H. (P.) xylabion*. Of course, there are so few heads known from the member that there is a possibility that the head belonging to the same species as the tails remains undiscovered. However, the fact that *H. (P.) tridentifera* has a quite similar morphology suggests that this is not correct. Finally, there is a good size match between the head and the tails.

The pits forming the V on the anterior part of the glabella are the external expression of the sites of muscle insertion. They form a much simpler pattern than those figured by Eldredge (1971), but this may be because they represent only the more definite insertion points.

H. (P.) xylabion can be distinguished from *H. (P.) tridentifera,* by its tuberculate glabella, the angular trace of the facial suture in front of γ and β, and by a proportionately narrower anterior glabellar lobe with respect to the more posterior lobes.

The specimens figured as *Synphoroides biardi* by Haas (1969), and referred to under the generic discussion, can be distinguished from *H. (P.) xylabion* by their granulose glabellar ornament and their more prominent median lobe on the anterior cephalic process.

Genus **Odontochile** Hawle and Corda, 1847

Type species.—*Asaphus hausmanni* Brongniart, 1822, from the Dvorce-Prokop Limestones (Pragian) of Bohemia.

Remarks.—In size, cephalic and pygidial outlines, shape of glabella, cephalic ornament, tuberculation of the pygidial rings and pleural bands, and the short pygidial spine, the species described below is comparable with the type species. The main difference between them lies in the deeper epi-border furrow on the type.

Odontochile (Odontochile) syncrama
new species

Pl. 28, fig. 5; pl. 29, figs. 1, 2

Types.—Holotype: OU 7197 from the Bois d'Arc Formation, Fittstown Member, at SW¼ sec. 35, T. 2 N., R. 6 E., Pontotoc County, Amsden collecting locality P16. Paratypes: OU 7196 from the same locality as the holotype; and OU 7198 from the Cravatt Member in the small quarry in SW¼SE¼ sec. 1, T. 1 N., R. 6 E., Amsden collecting locality P13.

Diagnosis.—Cephalic border has only a

slight anterior expansion; subocular platform is wide; glabella and inner fixed cheeks have scattered perforate tubercles with fine granules between; border and outer parts of cheeks have granules only. Pygidium has 17 complete rings and 15 or possibly 16 pleural furrows; border is wide and rather flattened; posterior pleural bands are weak and fade toward the border; anterior bands are much stronger, and the first few expand distinctly just inside the border; pleural furrows have an almost vertical front wall; interpleural furrows extend out onto border; anterior pleural bands have a single row of widely spaced perforated tubercles, with 6 or 7 on the 2d segment, decreasing to 1 or 2 on the 9th segment; border, and all pleural bands between the tubercles, are covered with granules; axial rings have tubercles the same size as those on the inner parts of the pleurae and arranged in a transverse row toward the back of each ring; in addition, the first 2 rings have 1 or 2 more on the anterolateral parts; 2d ring has a total of 10-12 tubercles; axis is well defined posteriorly; postaxial ridge is subtriangular in cross section; terminal spine measures only 4-5 mm long, is narrow, acute, and horizontally directed; doublure is steeply inclined and extends well inside the ends of the pleural furrows.

Remarks.—Only three specimens of this species are known: an external mold of a fragmentary cephalon, the internal mold of a pygidium that retains the impression of the terminal spine, and a skeleton-bearing pygidium that lacks the posterior extremity. The first two come from the same locality, and the character of the perforated tubercles suggests that they belong to the same species.

Although the cephalon is poorly preserved, it shows the characteristic features of an *Odontochile* in the spacing of the apodemes, the wide border with the shallow epi-border furrow, its glabellar outline and profile, its subocular platform, and the rounded anterior border without a process. The facial suture lies slightly outside of, and parallel to, the preglabellar furrow. The number of lenses in the eyes cannot be determined. The granulation between the tubercles on the glabella is best preserved around the margins of the anterior lobe and on the lateral parts of lobe 2p. However, there are scattered granules elsewhere, and I suspect that they originally covered the glabella but have been removed by abrasion. The surface of the free cheek below the ocular platform is dimpled and is covered with a dense mat of granules like those on the border.

Loss of the pygidial extremity on 1 specimen prevents an accurate count of the axial rings and pleural furrows, but there are 17 complete rings preserved on both, and there are 3 incomplete rings plus a terminus on the 2d specimen. There are 15 pleural furrows on the internal mold, and there may be another that is not reflected clearly on the interior. This is compatible with observations on the incomplete specimen. There may have been a few granules on the axial rings between the tubercles, but if so, only traces of them remain.

In terms of the trimorphism observed in *Huntonia* species, these specimens have a Type C morphology. It is possible, therefore, that some of the features listed in the diagnosis are not characteristic of the species as a whole.

This species clearly belongs to the same group as *O. litchfieldensis* (Delo), which is reported from the Sallsburg Quarry, Litchfield, New York, in rocks of Helderberg age. Only the pygidium of that species has been described, but it has the same distinctive ornament style as *O. syncrama.* I have examined the holotype, from which the following details are derived: There are 17 complete and 2 or 3 incomplete axial rings, plus a terminus; 14 pleural furrows; posterior pleural bands are much weaker than the anterior ones and fade abruptly near the border; anterior pleural bands have closely spaced perforate tubercles in a row along the crest, largest proximally and decreasing distally, where they are replaced by granules before reaching the border; posterior pleural bands are smooth or have scattered granules; borders are granulate, the granules extending onto the distal ends of the posterior bands only; axial rings have 1 or 2 large perforate tubercles at each end, and several smaller ones placed lateral to them on the first 7 or 8 rings; axis is well defined posteriorly; terminal spine is not preserved, but from the fragment of doublure present it is inferred to have been short, triangular both in outline and section, and directed almost horizontally.

Delo (1940, p. 46) placed *litchfieldensis* in

Dalmanites and compared it with *D. bisignatus* Clarke and *Odontochile micrurus* (Green). The former species is probably related, but the latter is not. *D. bisignatus* was first described from the Oriskany of Becraft Mountain, and it is in need of revision.

O. syncrama is distinguished from *O. litchfieldensis* by the much sparser tuberculation of its pygidial anterior pleural bands, by the presence of granules on both the anterior and posterior pleural bands right up to the axial furrow, and by the proportionately wider border.

Cravatt specimen.—A single small specimen OU 8269, from the Cravatt Member at Old Hunton Townsite, Amsden's locality C1-P, is probably a member of this species. Only half the pygidium is preserved, and the granulation is finer than on the types, so there is a possibility that it represents a separate subspecies. The cephalon is much more complete, and most of the thorax is preserved, so the following points may be added:

There is a definite swelling of the anterior border but no evidence of a process or a contraction of the border. Granulation covers the entire glabella, but it tends to be sparser and a little coarser on the medial part of the anterior lobe. The perforated tubercles are most abundant in the same region, and on the median part of the more posterior lobes, though they also occur scattered on the distal parts of these lobes. The palpebral lobe and palpebral area rise steeply out of the axial furrow and flatten out distally. Granules occur all over the palpebral region, and tubercles also occur on the palpebral area. The slender genal spine extends back at least to the level of the fifth thoracic ring. The cheeks have granules only. The doublure has a flat horizontal outer band and a steep inner one that lies beneath the border furrow. The 11 thoracic segments are typically dalmanitinid, the more posterior ones having a scimitar-like termination. They are granulate all over, and in addition they have up to 12 perforated tubercles irregularly arranged on each ring and 6 or 7 on the crest of each anterior pleural band. The pygidial rings show a definite but low median "hump," on and lateral to which there are up to 10 tubercles. The anterior pleural bands have 6 or 7 tubercles concentrated on the adaxial part, with a very occasional one on the posterior band.

Odontochile ceraunus, new species

Pl. 4, figs. 5-8

Types.—Holotype: OU 8264 from southwest of St. Clair Lime quarry, NW¼SE¼ sec. 14, T. 13 N., R. 23 E., Sequoyah County, Amsden collecting locality S6. Paratypes: OU 8265-8268, same locality.

Diagnosis.—Glabella shows low convexity in all profiles; facial suture lies well outside the preglabellar furrow; pygidium has 16-17 axial rings plus a terminus, the first 11 rings with apodemes; axis tapers almost to a point, the taper on the segments behind those with the apodemes being greater than that on the segments in front; overall angle of taper of axis measures 14°-16°; 12-13 pleural furrows are present; terminal spine is very short. Exoskeleton is thin and smooth except for a small area around the margin, which is granulate.

Description.—Glabella is about 30 mm long in largest available specimen; all glabellar profiles are weakly convex; occipital ring measures 0.7 times the width of the anterior lobe; apodemes 1p and 2p are transverse and deep and are not connected with the axial furrow; 3p also is moderately deep axially; facial suture lies outside the preglabellar furrow at a uniform distance; γ is opposite the midlength of lobe 3p; free cheek is steep beneath the ocular platform; lateral border is very wide, with a narrow convex inner band separated from a much broader flat outer band by an epi-border furrow that is really only a change in slope; anterior border is flat, semicircular in outline, unbroken by processes of any sort.

A few thoracic segments are preserved, and these show the normal dalmanitinid form.

Pygidium is peltate in outline; posterior is not well preserved on any specimen but probably has a terminal spine 2-3 mm long; axis has an overall taper of 14°-16°, with the posterior quarter tapering more abruptly than the remainder and producing a narrowly rounded terminus; there are 16-17 axial rings plus a terminus; apodemes on the 1st rings are wide, gradually narrowing down to the 11th, which is almost equidimensional; subsequent rings are without apodemes; there are 12-13 pleural furrows, all except the most posterior ones being strongly arched distally; the first 7 or 8 interpleural furrows are clear and divide the ribs in the typical dalmanitinid fashion; border is narrow, is not differentiated by a furrow, and carries pleural furrows almost to the margin; doublure has a flat outer band 3 mm wide on a pygidium about 40 mm long; inner band is almost vertical and is about 1 mm high in the same specimen.

Entire surface of exoskeleton is smooth except for the margin of the pygidial border, which is partly granulate on at least one specimen.

Remarks.—The material on which this species is based is rather fragmentary. No genal spines, pygidial extremities, or ocular structures have been preserved. Nevertheless, its thin, smooth exoskeleton makes it easy to recognize. This smoothness is a character that is rarely found in *Odontochile* but sometimes occurs in the Synphoriidae. The latter family also includes many forms with an abruptly tapering pygidial axis that is pointed posteriorly. However, all the diagnostic dalmanitinid characters listed in the discussion above are present, and there is no doubt that the species is correctly assigned to *Odontochile* as that genus is understood at present.

As far as I can determine, *O. ulrichi* Delo from the Lower Devonian of Nevada is the only described North American species to which this new species is comparable. Both have the same type of posterior contraction of the pygidial axis and are apparently smooth or very finely granulate. There are, however, similarities with two Kazakhstan species, *O. ulrichi asiatica* Maksimova and *O. arcuata* Maksimova (Maksimova, 1968). Both these species have similarly shaped pygidial axes, similar numbers of rings and pleurae, short terminal spines, and smooth surfaces. There are clear differences, particularly in the shapes of their pygidial pleurae and the width of their doublures, the pleurae of *O. ceraunus* being more curved distally and its doublure narrower.

The form described as *Odontochile* from the Rabbit Hill Limestone of Nevada by Haas (1969, p. 651) is similar to *O. ceraunus* in the shape of its pygidial axis, its curved pleurae, and its smooth surface, but although Haas considered it had a terminal spine, his plate 83, figure 4, suggests that there is a terminal embayment. Consequently, I am not sure that the generic assignment is correct. In any case, its doublure is wider than that of *O. ceraunus*.

?**Odontochile taffi** (Ulrich and Delo, 1940)

Pl. 30, fig. 4

Dalmanites taffi Ulrich and Delo; DELO, 1940, p. 50, pl. 3, fig. 27.

Type.—USNM 79037 from the Haragan Formation, west side of NW¼ sec. 21, T. 1 S., R. 8 E., Coal County.

Remarks.—The type specimen was taken from a collection made by Taff and Adams and is said to be from "the base of a terrace, 100 feet below the top of the Silurian Limestone." Presumably this limestone is the Bois d'Arc. I have examined this collection and others from a similar zone and have not seen a similar specimen. The only cephalons well enough preserved to identify in the original collection belong to *H. (H.) lingulifer*.

It is difficult, therefore, to interpret this species. It is unique in the following features: There are 16 complete and 2 incomplete rings plus a terminus; 15 pleural furrows, the last pair very close together on the flanks of the sharp-crested postaxial ridge; the axial furrow weakens abruptly at the posterior extremity, so that the crest of the postaxial ridge joins the axis, though the axis is generally clearly defined; there is a pair of small oval to circular pits on the first 12 axial rings, 1 in front of the inner end of each apodeme; distinct pseudo-half rings are developed on the first 11 axial rings; the ornament consists of uniform, fine granules over the whole surface, except the axial and pleural furrows; the doublure has a maximum width equal to the 6th axial ring, lies closely oppressed beneath the dorsal border, and has a very slight upturned inner edge.

Without a cephalon, this species cannot be assigned to a genus. Maksimova (1972, p. 92) regarded it as a member of her subgenus *Odontochile* (*Reussia*), presumably because of its doublure width. The doublure is certainly a remarkable structure on *taffi,* being quite unlike any species from North America of which I am aware. However, although the axis is narrow and short like other species of *O.* (*Reussia*), its doublure is not as wide relative to the axis as in these species.

Genus **Phalangocephalus,** new genus

Type species.—Dalmanites dentatus Barrett, 1876, from the Port Jervis Limestone, Trilobite Mountain, Port Jervis, New York; Siegenian.

Diagnosis.—Cephalon is moderately convex; glabellar lobes 2p and 3p are not elevated above the general level of the glabella; furrows 2p and 3p are continuous with the axial furrow; palpebral furrows are more or less V-shaped in outline; eye is situated opposite glabellar lobes 2p and 3p; eyes are raised above glabella and surmounting a prominent platform; posterior border furrow is deep and steep walled; lateral border furrow is only lightly impressed; lateral and anterior borders bear a number of flattened spines, with the longest and most acute ones situated medially and decreasing progressively in size toward the genal region; genal spines are slender and very acute; tubercles are present on the glabella, on at least part of the cheeks, and on lateral parts of the posterior border. Anterior pleural bands of thorax are larger than the posterior ones; pleural furrows are deep and extend onto the pleural tips; pleural spines are well developed. Pygidium is moderately arched; there are about 15 axial rings and about 10 pleurae, the most posterior pair with their proximal ends opposite ring 11 and directed back parallel with the axis; interpleural furrows are deeply impressed except at their distal extremities; border is very narrow or is absent; terminus is upswept and produced into a prominent, broadly based spine; axial rings have 2-5 tubercles; anterior and posterior pleural bands each display a single row of tubercles; fine granules are present over most of the surface except the pleural furrows.

Remarks.—Certain points of the above diagnosis need comment. The features of the thorax and pygidium mentioned are taken from the type species only, these structures being unknown for *P. rutabulum*, new species. The tubercles on the glabella are definitely perforated in *P. rutabulum*, but the available material of *P. dentatus* is not good enough for certain identification of perforations, though they are probably present. This feature may be another useful generic character.

P. dentatus has previously been placed in the genus *Corycephalus* Hall and Clarke (Hall and Clarke, 1888; Delo, 1940), the type species of which is the poorly known *Dalmanites regalis* Hall, an assignment that seems to have been based on the presence of a large number of cephalic marginal spines in both species. However, *C. regalis* has important differences, such as the greater convexity of the cephalon, the peculiar glabellar lobation with its grossly inflated and laterally extended lobes 2p and 3p, and the orientation of the marginal spines, which are directed downward rather than outward. In addition, the thorax and pygidium of *C. regalis* are virtually unknown. Under these circumstances, the possession of the marginal spines cannot be regarded as evidence of close relationship.

P. rutabulum is significantly older than *P. dentatus* (see below). Assuming that the differences between these two species can be used to define "trends" that can be projected back in time, the ancestor of *Phalangocephalus* would be a species of *Dalmanites* having a smooth cephalic margin (or perhaps a slight anterior projection); tuberculate cephalic ornament; a strong, deep posterior border furrow; about 30 files of lenses in the eyes; and facial sutures that cut in close to the glabella anteriorly. In addition, the pygidium probably had a triangular outline with straight sides, and the more posterior pleurae were probably directed parallel with the axis. No such species is known to me at present.

Species assigned.—*P. dentatus* (Barrett) and *P. rutabulum,* new species.

Age.—The Port Jervis Limestone (Shimer, 1905; Boucot and Johnson, 1967) is of Siegenian age, and the Bois d'Arc is Gedinnian.

Phalangocephalus dentatus (Barrett)

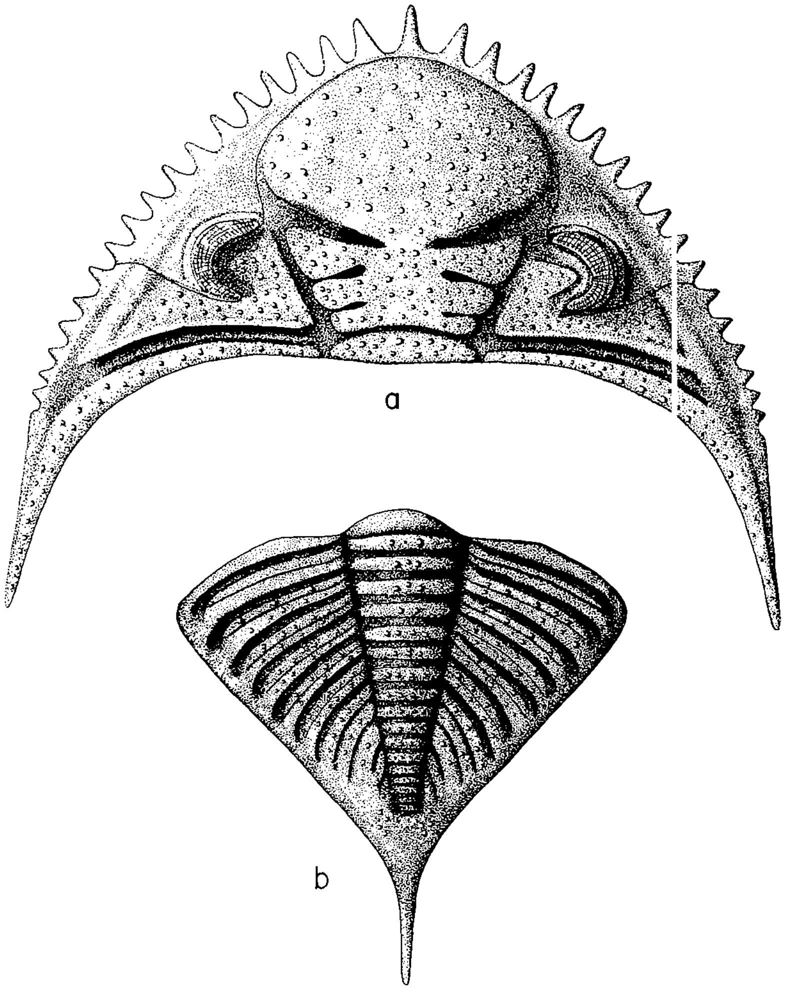
Pl. 31, figs. 1-8

Dalmanites dentata Barrett, 1876, p. 200, pl. 7.
Dalmanites (Corycephalus) dentata Barrett; Hall and Clarke, 1888, p. 58, pl. 11A, figs. 4-6.
Corycephalus dentatus (Barrett); Delo, 1940, p. 72, pl. 8, figs. 8-9.

Types.—As reported by Delo (1940, p. 72), the original material of Barrett has been lost. The specimens figures by Hall and Clarke (1888, pl. 11A, figs. 4-6) are now cataloged as 4310-11 in the New York State Museum.

Diagnosis.—Cephalic border has 37 spines, the longest medial and the shortest on the flank of the genal spine; anterior border is very short (sag. and exsag.) and steep; tubercles are present on the glabella, on the fixed cheeks inside the border furrows, and on the posterior border; tubercles and spaces between are covered with coarse granules; remainder of cephalon is covered with fine granules; eye has approximately 175 lenses arranged in approximately 27 files; palpebral lobe rises gently from the axial furrow; thoracic segments have acute tips on the pleural spines; pygidium has a prominent, gently to strongly upswept caudal spine; there are 15-16 axial rings plus a terminus, and 10-11 pleurae; a pair of moderately strong tubercles is present on each axial ring and 1 or 2 smaller ones on either side of these; there are 4-6 small tubercles on each anterior and posterior pleural band.

Description.—Cephalon is well rounded to ogival in outline. Glabella is as wide as long; width increases gradually from the occipital furrow to the midlength of lobe 3p, then even more gradually to the midlength of the anterior lobe; axial furrow is deepest opposite lobes 1p and 2p, shallowest opposite the midpoint of lobe 3p, and is marked only by a change of slope around the front of the anterior lobe; occipital ring is longest medially, and occipital furrow has a slight flexure forward medially; 1p is the smallest of the lateral glabellar lobes; furrow 1p has a slitlike apodemal pit and is interrupted medially by ornament; apodemal pit of furrow 2p forms a broad, inverted V, is clearly



Text-figure 29. Reconstruction of cephalon (*a*) and pygidium (*b*) of *Phalangocephalus dentatus* (Barrett).

joined to the axial furrow, and is joined axially with its fellow by a broad but distinct furrow; axial part of furrow 3p lies a short distance in front of 2p and is connected to it by a broad depression; lateral part of 3p expands abruptly (probably to carry a large flat muscle scar). Axial part of glabella between lobes 1p and 3p is slightly raised above the lobes themselves but does not form an "axial lobe"; anterior lobe forms the highest part of the glabella. Palpebral lobe is U-shaped in outline and rises a little above the highest point of the glabella; palpebral furrow is rather V-shaped in outline, rising from the axial furrow at its shallowest point opposite 3p, and gradually fading in strength posteriorly. Eye is preserved on 1 specimen only; in dorsal view the curvature of the visual surface increases posteriorly; there are an estimated 27 vertical files of lenses; the lens pattern is not clear, but counting from the anterior it is approximately 3, 3, 4, 5, 6, 7, 7, 7, 7, 8, 8, . . . 8, 8, 7, 7, 6, 6, 5, 4, 3; maximum height of the visual surface is at the median files, toward the bottom of which the lenses reach their maximum diameter of 0.4 mm; at the top of these files and in the terminal files, lenses decrease to 0.25 mm in diameter; eye is defined at the base by a sharply incised furrow and surmounts a sharply defined horizontal platform extending from the anteromedian end of the eye to about the 10th file from the rear, where it abruptly terminates. Anteriorly, facial suture lies in, or just in front of, the change in slope that marks the edge of the glabella; medial junction between the two limbs is subangular; β is well rounded and lies just outside the axial furrow; δ-δ passes through the anterior edge of the 2p apodemes; ϵ is highly acute; lateral to ϵ, suture is gently sinuous; ω is between border spines 11 and 12, numbered from the front. Posterior border furrow is very strong, is lanceolate in outline, and its anteromedial edge lies opposite the occipital apodeme; between the axial furrow and the fulcrum, the posterior and the higher anterior walls of the furrow are quite steep, almost vertical, and the base is rounded; lateral to the fulcrum, the anterior wall becomes progressively less steep, but the posterior wall remains nearly vertical; furrow fades away on base of genal spine. Posterior border is about half the length (exsag.) of the occipital ring adaxially, becomes even shorter toward the fulcrum, then lengthens abruptly until it turns onto the genal spine.

Fixed cheek has a sharply defined crest against the posterior border furrow and slopes gently forward from this; free cheek drops away quite steeply beneath the eye platform and then flattens out slightly into the border furrow. Lateral border furrow is shallow and vaguely defined; it meets the axial furrow behind β and fades away posteriorly just in front of the lateral extremity of the posterior border furrow. Lateral border is narrow, gently convex, and is separated from the marginal spines by a distinct furrow (the epi-border furrow) that continues down the length of the genal spine. There are 37 marginal spines that are long and acute medially but become progressively shorter and more obtuse posteriorly. Genal spines (measured from a line joining the fulcra) are a little shorter than the glabella; in both lateral and vertical views, they are very slender posterior to the last of the marginal spines; inner face is almost vertical.

Glabella is covered with tubercles, is circular to ovate in outline, and measures up to 1.2 mm in diameter on a specimen of glabellar length of about 27 mm; coarse granules cover the surface of the glabella on and between the tubercles; a shallow, ovate pit lies behind the midpoint of the anterior lobe; tubercles, somewhat smaller than those on the glabella, cover the posterior border, the fixed cheek inside the border furrows, and the palpebral area; borders, marginal spines, and free cheek below the eye platform are finely granulate.

Doublure is longest (sag.) medially; hypostomal suture is more or less straight between an exsag. line through the two spines on either side of the median, then is arched evenly back to a point opposite spine 5, where it terminates; lateral to this point the doublure consists of a vertical inner portion and a highly convex lateral portion, which really forms a narrow ridge; between the extremities of the hypostomal suture is a broad, shallow furrow; the surface of the doublure and the ventral surface of the spines are finely granulate. Hypostome is unknown.

Thorax apparently has 11 segments; axis is not well known; pleurae extend into spines; pleural furrow is deep and steep walled, narrow adaxially, widest at the fulcrum, and extends well onto the pleural tip; anterior band is larger and higher than the posterior band; ornamentation is unknown.

In dorsal view, pygidium is triangular, with almost straight sides, and is produced into a strong caudal spine; in lateral view, crest of axis is almost straight, and caudal spine is upswept; caudal spine is flat based and has a slightly angular crest; axis of pygidium tapers evenly and is poorly defined posteriorly; there are 15 or 16 transverse axial rings, plus a terminal piece; pleural furrows number 10 (possibly 11), the anterior ones being transverse adaxially but deflected back strongly at their distal ends, and the posterior 2 (or possibly 3) are directed backwards over their entire length; intermediate ones have intermediate shape; 10th pleural furrow meets the axial furrow opposite the 12th ring; pleural furrows is narrowest adaxially, slightly broader distally, and fades away gradually to the border; interpleural furrows are strong at least as far back as the 8th; adaxially the posterior and anterior pleural bands are of approximately equal strength, but distally the posterior one diminishes rapidly, whereas the anterior one expands. Border is narrow, is on the same slope as the downturned ends of the pleurae, and is not separated off by a border furrow. Each ring has a pair of slightly enlarged tubercles, one on either side of the axis; first few rings each have a smaller axial tubercle set slightly in front of this pair; 1 or 2 smaller tubercles are present on each ring lateral to the major part; anterior and posterior pleural bands each have a row of 4 to 6 small tubercles; remainder of surface (except furrows) is finely granulate; only a small part of the narrow steep doublure was observed. The following tables give the dimensions, in millimeters.

Cephala

Axial length	Length, including genal spines	Length of anterior spines	Length of glabella	Width of glabella
27	ca. 48	ca. 4	21	23
23	ca. 35	–	19	16.5
21	ca. 32	ca. 3	17	18
–	–	–	12.5	10.5

(Specimens 1 and 3 may have been somewhat flattened, thus accounting for their relatively greater glabellar widths.)

Pygidia

Total length	Length of axis	Total width	Width of axis
ca. 29	20	ca. 30	9.5

(This is a form with a short caudal spine (see below). No long-spined forms are sufficiently complete to measure.)

Remarks.—This description is based on the two specimens figured by Hall and Clarke (1888, pl. 11A, figs. 5-6), together with 15 isolated cephala and pygidia from Port Jervis provided by Dr. Niles Eldredge. The more or less complete specimen figured by Hall and Clarke has not been seen. Most of this material is preserved as steinkerns, since the exoskeleton "peels off" when the rock is broken, and much of it is slightly deformed. Nevertheless, it is adequate to provide much new information and to correct previous descriptions. No thoraxes have been available to me, though there is one broken segment probably belonging to the species. I have therefore had to rely on the accuracy of the figure given by Hall and Clarke (1888, pl. 11A, fig. 4) and the description of Barrett.

There are some minor discrepancies between the description given above and that given by Delo (1940). There are certainly more axial rings and fewer pleurae on the pygidium than he indicates. The posterior border furrow does not parallel the posterior border of the cephalon, there being a strong divergence lateral to the fulcra. Nor is there any evidence of a furrow along the posterior border of the cephalon, as is shown by Hall and Clarke (1888, pl. 11A, fig. 5).

The cephalic doublure described above is unusual, not only in the great width of the hypostomal suture but also in the narrow strip of convex surface lying between the vertical inner band and the lateral marginal spines, and in the proximity of the antennal furrow to the bases of the anterior spines (see pl. 31, fig. 5). These features, together with the position of the epi-border furrow, indicate that the marginal spines have been developed by the indentation of a once wide and continuous border, rather than by the outgrowth of the spines from the original border.

There appears to be some evidence that there are two types of caudal spine represented in the collection: a shorter type upswept at about 10° to the horizontal and a much longer type upswept at 20°-25°. There is not enough material to be certain of the existence of two discrete groups. As far as I can determine, there is no cephalic dimorphism.

Phalangocephalus rutabulum
new species
Pl. 30, fig. 5

Holotype.—OU 6593 from Cravatt Member of the Bois d'Arc Formation in Bois d'Arc Creek.

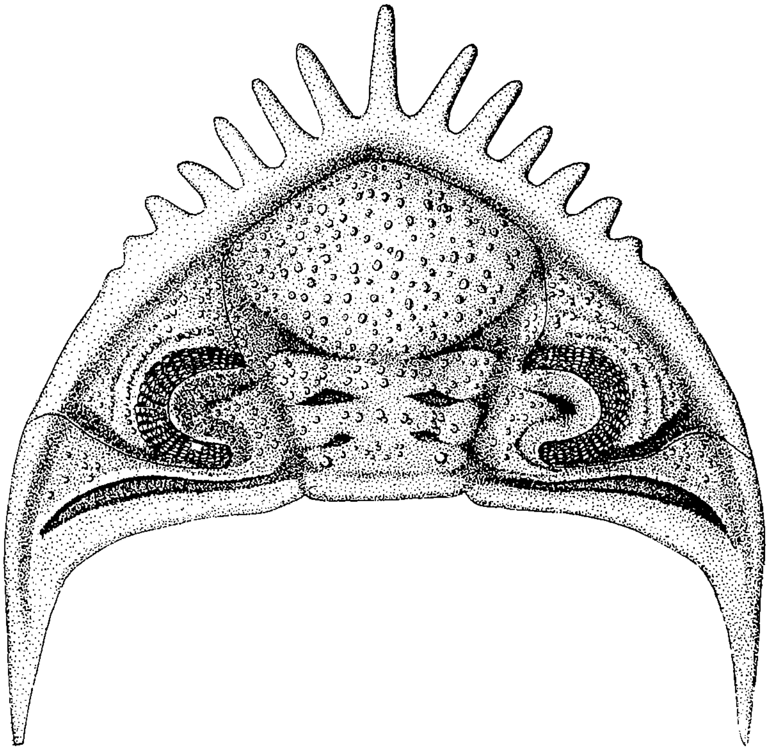
Diagnosis.—Glabellar width and length are approximately equal; anteriorly there are 13 marginal spines, the median one longest and most pointed, the lateral ones progressively shorter; palpebral lobes are raised high above the glabella; tubercles cover the whole cephalon except the furrows and the anterior and lateral borders.

Description.—Cephalon (exclusive of genal spines) is twice as wide as long; outline tends to be subtriangular but still moderately rounded. Glabella is as wide as it is long; width increases from the occipital furrow to the midpoint of lobe 3p, with this width maintained to the front of furrow 3p, and expanding finally around the anterior lobe. Occipital ring was not completely preserved, but apparently was very short; occipital furrow is short, curved forward medially; furrow 1p has a deep adaxial apodemal pit set slightly obliquely to the midline, connected to the axial furrow by a shallow groove, connected with its fellow by an even shallower groove; apodemal pit of furrow 2p is in the form of a shallow inverted V, is clearly connected to the axial furrow by a shallow groove directed obliquely backward, and is joined to its fellow by a vaguely defined depression; apodemal pits 3p are slitlike and are directed obliquely forward laterally, the furrow becoming very broadly triangular. Lobes 2p and 3p stand a little higher than the part of the glabella between them, but there is no sign of longitudinal furrows; anterior lobe stands higher than remainder of glabella. Palpebral lobe is U-shaped in outline and rises from the axial furrow at about 45°, flattening out distally so that its tip is almost horizontal; palpebral furrow is deeply impressed, V-shaped in outline, and connected to the axial furrow by a narrow, shallow groove. Facial suture swings back in a shallow arc adaxially from ω, almost reaching the posterior border furrow behind the eye; ϵ and γ are on broad, almost vertical arcs; there is an abrupt outward swing in front of γ, and then it becomes parallel to the axial line to β, meeting its fellow at a subangular medial junction.

Eye is poorly preserved; it is highest at its midlength, decreasing in height more gradually to the front than to the back; an estimated 30 files of lenses are present; number of lenses in files is unknown in detail, but the maximum number probably is 8; base of eye is defined by a sharply incised furrow; a broad, almost flat platform around anterior two-thirds of eye abruptly narrows at both front and back; there is a narrow, depressed band on the free cheek, parallel to the posterior facial suture from the eye platform to the border furrow.

Posterior border is short (exsag.) adaxially, increases gradually in length beyond the fulcra, and swings back on to the genal spine; lateral border is broad, rising to a crest from the border furrow, then falling away in a concave surface to the margin; anterior border does not have these areas differentiated; 13 flattened, anteriorly directed spines develop from the border, the longest and narrowest placed medially with the remainder becoming progressively shorter and blunter laterally; median spine is about 4 mm long and 1.5 mm wide at its base. Posterior border furrow is distinctively shaped, lanceolate in outline, with a vertical anterior wall, a lower and less steep posterior wall, and an almost flat base; only the base of the genal spine is preserved, but from contours it must be at least 10 mm long.

Ornament consists of apically perforate tubercles on all glabellar lobes and occipital ring; no ornament is seen between tubercles, but their crests, particularly those on the anterior lobe, are covered with very delicate granules; a slightly enlarged tubercle is present laterally on 1p. Tubercles are also present on fixed and free checks inside the border furrows, excepting (a) the ocular platform; (b) the depressed area parallel with the suture, both of which regions are smooth; and (c) the palpebral lobe outside the palpebral furrow, which is finely granulated; margin of ocular platform is outlined by a row of slightly enlarged tubercles, forming a distinct rim. Crest of anterolateral part of border and lateral part of posterior border have an irregular row of smaller tubercles; unlike the glabella, cheeks have extremely delicate granules between the tubercles; fine granules are also present on



Text-figure 30. Reconstruction of cephalon of *Phalangocephalus rutabulum*, new species. Genal regions have been reconstructed by reference to *P. dentatus.*

lateral border, base of genal spine, and anterior spines with the granule size increasing slightly toward the margins.

Ventral surface of the cephalon, the thorax, and the pygidium are unknown.

Dimensions.—

Medial cephalic length (incl. process)	22 mm
Cepahlic width (estimated)	42 mm
Glabellar length	16 mm
Glabellar width	16 mm

Remarks.—The single specimen of this species is preserved as an external mold in a piece of white chert. The detail is exquisite, but only a fragment remains. The shape of the genal spines on the accompanying text-figure is largely inferred from the contour of the preserved basal sections.

The specimen is readily distinguished from *P. dentatus* by its flatter glabellar profile; fewer border spines; higher, shorter eyes; finer, more numerous tubercles on the glabella; tubercles on the free cheek below the eye; deep furrow parallel with the posterior limb of the facial suture; and wider, flatter anterior and lateral borders inside the marginal spines.

Dalmanitacean, genus and species undet.

Pl. 28, fig. 1

Material.—OU 6594Z from the Frisco Formation, southwest of St. Clair Lime Quarry, NW¼SE¼ sec. 14, T. 13 N., R. 23 E., Sequoyah County.

Description.—A single broken pygidium is known, and it must have been more than 65 mm wide and more than 50 mm long. Its posterior outline is approximately semicircular, and overall profiles are gently convex, the axis being more strongly convex than the pleurae. There are 9 rings and a rounded terminus preserved. The rings are highest at the back and slope gradually into deep, long furrows. The anterior rings carry a row of 10 tubercles across their posterior edges, but this number gradually decreases on subsequent rings. The pleural furrows are open V shaped in section and are directed posterolaterally in faint axes. They fade abruptly toward the broad, flat border. There are 7 furrows associated with the 9 rings, but interpleural furrows have not been observed. Along the crest of the anterior pleural band is a row of tubercles like those on the axis, and scattered similar tubercles occur on the posterior band. The doublure is unknown.

Remarks.—No form like this has been described previously. It is clearly a dalmanitacean, but its mode of segmentation and its outline are unique for that group. Its doublure and anterolateral corners are unknown, so it is not possible to determine its family relationships with certainty. The wide flat border and rounded posterior extremity suggest that it belongs neither to the Dalmanitinidae nor to the Synphoriinidae.

Corycephalus is the only dalmanitacean, of which I am aware, with a cephalon that would be matched on enrollment by a pygidium of this shape. As has been indicated above, the pygidium usually figured for this genus is that of *Phalangocephalus dentatus,* the triangular shape of which would not complement the broadly rounded outline and ventrally directed palisade of marginal spines exhibited by *Corycephalus regalis*. The cephalon of that species is abnormal in many other respects—convexity, glabellar lobation, slender genal spines—so that it would not be surprising if its pygidium was also abnormal. Dr. Niles Eldredge informs me that none of the topotypic specimens of *regalis* qualifies as a pygidium of the species, and hence it is impossible to check the appropriateness of the above suggestion.

Suborder CALYMENINA Swinnerton, 1915
Family CALYMENIDAE Burmeister, 1843
Subfamily CALYMENINAE Burmeister, 1843
Calymeninid, genus and species undet.

Pl. 1, fig. 6

Description.—A single pygidium 8.5 mm wide is available. It has 8-9 axial rings plus a terminus, and 5-6 pleural furrows. The notch in the posteroventral margin for the reception of the hypostomal medial knob is abnormally large. The surface is poorly preserved, but it appears to have been almost smooth.

Remarks.—This specimen is of normal calymeninid type and is probably referable to *Calymene* itself or to *Gravicalymene*. It is the only representative of the whole suborder in the Haragan-Bois d'Arc fauna.

Material.—OU 8259 from the Clear Hill section, NE¼ sec. 4 T. 2 N., R. 6 E., Pontotoc County, Amsden collecting locality P3-JJ.

Suborder CHEIRURINA Harrington and Leanza, 1957
Family CHEIRURIDAE Salter, 1864
Subfamily CHEIRURINAE Salter, 1864
Genus **Cheirurus** Beyrich, 1845

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

?**Cheirurus** sp.

Pl. 1, fig. 3

Description.—Glabella expands only slightly between the occipital ring and furrow 3p; frontal lobe is expanded; the ratio width of frontal lobe/width of occipital ring is 4/3; occipital ring is approximately twice as long medially as at the axial furrow; lobe 1p measures approximately 0.22 times the total glabellar length; axial, occipital, and all glabellar furrows are narrow and are not deeply incised; furrow 1p curves back to make a strong junction with the occipital furrow; furrow 2p curves backward slightly medially; 3p also is directed slightly backward but is almost straight; furrows 2p and 3p are distinct to within 1 mm of the midline, where they abruptly become almost imperceptible; preglabellar furrow is distinctly impressed laterally but is almost indistinguishable medially.

Posterior border is highly arched and is uniform in length (exsag.) throughout; posterior border furrow is very short (exsag.) and is sharply incised axially, increasing in length to a maximum in front of the fulcrum, and then diminishing laterally, to disappear at the lateral border furrow; base of furrow is flat or slightly arched; lateral border is well rounded; genal spine is depressed oval in cross section, rounded at the tip, and one-seventh the length of the glabella.

Facial suture shows ω approximately opposite the end of the posterior border furrow; ϵ is rounded and lies opposite the abaxial end of furrow 2p, and γ is on a very slight curve opposite the abaxial end of furrow 3p; β is just outside the axial furrow; anterior limb of suture converges slightly on the preglabellar furrow axially.

Palpebral lobe is small, slightly raised, well rounded in outline, and is situated opposite the posterior part of lobe 3p; palpebral furrow meets the axial furrow in front of furrow 3p, is only slightly flexed crossing the palpebral lobe, then arches laterally into a postocular furrow parallel with the posterior limb of the facial suture, where it fades away; a row of pits is present in the furrow behind the midpoint of the palpebral lobe.

In general, the size of the pits on fixed cheek increases laterally; a prominent pit is present in the lateral border furrow just behind the facial suture, and there is another in the palpebral furrow opposite δ; a few small pits are also present laterally in the posterior border furrow; a protuberance on cheek opposite furrow 3p is slight.

Ornament consists of fine granules on genal spines, on lateral border, and on at least the posterior part of the posterior border; glabella apparently is smooth but may have been finely granulose.

Dimensions.—		
	Glabellar length	17.5 mm
	Cephalic width	28.5 mm
	Maximum glabellar width	13.0 mm

Remarks.—This specimen has had at least some of the detail on the surface destroyed, but the macrostructures are still well preserved.

In the absence of the rostral plate, hypostome, thorax, and pygidium, it is not possible to be certain of the generic assignment. The incomplete glabellar furrows 2p and 3p exclude it from *Crotalocephalus, Crotalocephalina*, and *Crotalocephalides*, the only genera of the Cheirurinae known from the Early Devonian (Lane, 1971). On the other hand, these furrows are more nearly complete, and the eyes are placed farther forward, than on typical species of *Cheirurus. Didrepanon* Lane, 1971, has furrows 2p and 3p of a similar shape to those of the Cravatt specimen, but the type species has its eyes farther back and the preglabellar furrow is continuous (Lane, 1971, pl. 4, fig. 15a). The Silurian genus *Chiozoon* Lane, 1972, has a similarly shaped glabella and anteriorly situated eyes. However, its glabella is proportionately narrower, its facial suture reaches the lateral margin in a more anterior position, and its furrows 1p do not effect a strong junction with the occipital furrow medially. Until further specimens become available, it is considered best to refer the Oklahoma species tentatively to *Cheirurus.*

Ormiston (1972, pl. 1, fig. 17) figured a specimen from the Siegenian Windmill Limestone of Nevada as an unnamed species of *Cheirurus*. Its glabellar furrows, genal spine, and anterior eyes are quite similar to those of the Cravatt specimen, but its anterior glabellar lobe is apparently less rounded laterally.

I know of no other species with which this form can be closely compared. It differs from *Cheirurus infensus,* found in the Henryhouse Formation in the same region, in its proportionately narrower frontal lobe, the more delicate lateral glabellar furrows, the connection of the palpebral furrow with the axial furrow in front of furrow 3p rather than behind it, the more anterior position of the palpebral lobes, the transverse rather than anterolateral direction of the posterior limb of the facial suture from the eye, the fewer pits on the lateral parts of the fixed cheeks, and the very short genal spines.

Material.—OU 6549 from the Cravatt Member, east side of Goose Creek, NE¼SE¼ sec. 26 T. 1 N., R. 7 E., Coal County, Amsden collecting locality P17-D.

Cheirurinid, genus and species undet.

Pl. 1, fig. 4

Description.—Hypostome is almost complete; length approximately equals width; middle body is subquadrate posteriorly, moderately convex, and is surrounded by border furrows that are deepest laterally and distinct but shallow posteriorly; anterior border furrow is sharply incised; middle furrow is very weak; antennular notch is located at about one-third the length from the anterior margin; anterior border continues as a very narrow band around the anterior margin; lateral border is widest just behind the shoulder and has a slightly concave outer edge; posterior border is not well preserved; most of surface is slightly worn, but anterior part of middle body is smooth.

Remarks.—This is the only cheirurinid known from the Fittstown Member. It has the characters of the members of the Cheirurinae. Since the Fittstown and Cravatt Members of the Bois d'Arc Formation are partly contemporaneous, it is possible that this specimen belongs to the same species as the cranidium described above.

Material.—OU 7191 from the Fittstown Member, Bois d'Arc Creek, SW¼NW¼ sec. 11, T. 2 N., R. 6 E., Pontotoc County, Amsden collecting locality P8-F, 16 feet above the base.

Order ODONTOPLEURIDA Whittington, 1959

Family ODONTOPLEURIDAE Burmeister, 1843

Subfamily ODONTOPLEURINAE Burmeister 1843

Genus **Leonaspis** Richter and Richter, 1917

Type species.—*Odontopleura leonhardi* Barrande from the Kopanina Beds (Ludlovian) of Bohemia.

Remarks.—Attempts by Prantl and Přibyl (1949) and by Alberti (1960) to split this large and variable genus have not been generally accepted. They have been based largely, but not entirely, on the dimensions of the pleural spines in various parts of the thorax.

At present I can see no clear morphological, temporal, or geographical patterns that would permit a more rational subdivision. However, the following points are worthy of note.

1. Species with four marginal spines between the dominant pair on the pygidium seem to be absent from the North American Silurian-Devonian.
2. As noted by Clarkson (1969b, p. 333, the free cheeks of some species of *Leonaspis* have marginal spines that are "outwardly splayed rather than vertically directed," as in *L. deflexa*.
3. Hypostomes of the type found in *L. williamsi* Whittington, *L. tuberculata* (Hall), and *L. clavata* Chatterton are quite different from that described by Bruton (1967) for *L. crenata* (Emmrich) from the Silurian of Gotland. The main differences are in the pointed form of the posterior border, the incomplete border furrow, and the markedly anterior position of the middle furrows in *L. crenata*.
4. The anterior spines on the third and subsequent thoracic segments, which in most odontopleurid genera are rather constant in form, show a large range in variation. Compare, for example, those described by Ormiston (1967, p. 54, pl. 5, fig. 2), which have a strongly bifid shape, with those known from *L. williamsi, L. tuberculata,* and *L. clavata,* which have a basically trifid to quadrifid form.

Dimorphism.—At first sight, the presence of 2 or 4 spines between the dominant marginal spines on the pygidia of *Leonaspis* suggests that this is a form of sexual dimorphism. However, there are two objections to this view, neither of them conclusive. In the first place, some species for which large collections have been obtained from single localities contain only one type of pygidium. An example is *L. williamsi* itself. All this may mean, however, is that this kind of pygidial dimorphism is not general throughout the genus. In the second place, when the two types do occur together, the species bearing them sometimes have other, apparently unrelated, differences. Compare, for example, *L. rattei* and *L. jenkinsi* in the table given by Chatterton (1971, p. 46). It could be argued that, taken together, the differences listed indicate genuine specific differences.

A stronger case can be made for a different type of dimorphism in *L. leonhardi*. Bruton (1968, p. 20) records pygidia that are smooth or finely pustulose and others that are coarsely granulate, both associated with identical heads. This kind of ornamental dimorphism is found commonly in arthropods and is found also in phacopid trilobites.

For *L. williamsi,* the argument is stronger. From a total collection of 40 specimens for which significant parts of the cephalon and thorax are available, 16 belong to the holotype group (Type A) and 21 to a 2d group (Type B). Three seem to be intermediate. These forms occur together at the Old Hunton Townsite and White Mound localities, but they occur in very different proportions. At Old Hunton there are six Type A to each Type B, and at White Mound the ratios are reversed. A further complication is that they almost certainly occur in more than one bed at each locality. The specimens have a community of characters that induced Whittington (1956b) to include them in the one species without comment. The 3 main differences between the 2 groups are:

1. Type A has a single, and Type B a double, row of tubercles down the thoracic pleurae.
2. Type A has 8 or 9 thoracic segments, and Type B invariably has 8. This is presented in tabular form below (table 5).
3. Type A has a few tubercles, if any, in the librigenal border furrows, whereas Type B has tubercles of uniform density over the librigenal surface.

The three intermediate forms have cephalic ornamentation similar to Type B, and a single row of tubercles on all or most thoracic pleurae like Type A. It is probably significant that the two specimens on which the pleural spines are preserved (OU 5276 and OU 6532) have small tubercles on their crests. This is also a Type B character. OU 5276 also has paired tubercles on the left side of the 5th segment and on both sides of the 6th, and OU 6532 has accessory tubercles on the anterior pleural bands of the 7th and 8th segments. OU 5276 has the pygidium preserved, and it is a typical Type B form. It also has eight thoracic segments. The other specimen is not as well preserved and does not have a pygidium. This evidence is not indicative of the hybridization of two species, but suggests instead that these specimens are aberrant Type B forms.

There is one other minor complication. The paratype figured by Whittington (1956b, pl. 58, fig. 1), which in all other respects is a normal Type B, has a single spine between the dominant marginal spines on the pygidium. This pattern has not been observed on any other specimen nor on any other species of *Leonaspis*. I can only conclude that it is an abnormality.

TABLE 5.—NUMBERS OF SPECIMENS OF *Leonaspis williamsi* OF TYPES A AND B WITH 8 OR 9 THORACIC SEGMENTS

	Specimens counted	No. with 8 thoracic segments	No. with 9 thoracic segments
Type A	13	7	6
Type B	14	14	0

Leonaspis williamsi Whittington, 1956

Pl. 32, figs. 1-7; pl. 33, figs. 1-9; pl. 34, figs. 3-5

Leonaspis new species; WHITTINGTON, 1956a, p. 206-207, fig. 7.

Leonaspis williamsi WHITTINGTON, 1956b, p. 509-510, pl. 57, figs. 10-16; pl. 58, figs. 1-4, 6, 7.

Diagnosis.—Cranidium has a longitudinal furrow that is continuous, but it is much weaker opposite lobe 1p than 2p and is deepest at the junction with furrow 1p; occipital ring has an enlarged median tubercle but no spine; surface of cranidium and free cheeks have rounded tubercles but no granules; there are 13 marginal spines on the free cheeks, the most anterior ones very short and squat, the more posterior ones longer and more slender, and those on the genal spine thornlike; 2 spines are present on the dorsal surface of the genal spine; 10 to 14 tubercles are present on the anterior margin of the cranidium, the median ones being very small; genal spines are only slightly curved. Hypostome has continuous border furrow; middle furrow lies at about one-third the length of the hypostome; marked tubercles occur on the middle body anteriorly. The 8 or 9 thoracic segments have 2-6 prominent tubercles on each ring, and 1 or 2 on each pleura; anterior pleural spines are trifid on segments posterior to the 3d. Pygidium has 2 marginal spines between the dominant pair and 3 outside; axis and pleurae are tuberculate.

Description of Type A.—A basic description is given by Whittington (1956b), and supplementary information only is given here.

Cranidium narrows markedly toward the anterior margin, with α-α approximately equal to the glabellar width across the anterior of lobes 2p; ω-ω is approximately 2.5 times the length of α-α. The eye ridge abuts the suture below the eye and diverges inward from it only when opposite the posterior end of lobe 2p. There is an irregular row of tubercles on it, the anterior ones being the larger. The palpebral furrow runs from the back of the palpebral lobe to opposite the middle of lobe 2p, where it joins the axial furrow. Between the palpebral furrow and the axial furrow there is a single row of 4 or 5 tubercles. Lateral glabellar lobe 1p tends to be smooth medially but has a few tubercles front and back; lobe 2p is tuberculate all over; longitudinal furrow is weakest opposite lobe 1p, definitely deeper opposite lobe 2p.

Occipital ring has a moderate posteromedian tubercle flanked on each side by 2 or 3 much smaller tubercles and with an arc of 4-6 small variable tubercles around its front; a few very fine tubercles are present on the base of the posteromedian tubercle. Posterior border has 1-10 tubercles of highly variable size. Anterior border has 10-14 small tubercles, more or less anteriorly directed, somewhat irregular in size and spacing. Marginal spines on free cheek usually number 13; they are short, squat, and have granules over their tips anteriorly; posterior spines become progressively more attenuated. Border furrow on free cheek is generally smooth or has traces of radial furrows and ridges. Border itself is low and rounded posteriorly but flattens out even more anteriorly. Tubercles on lateral border are quite variable; some specimens have a single row throughout, others have 1 row in front and 2 or 3 rows toward the rear, but they are always well scattered. Eye stands on a low pedicel and in horizontal section covers about 200° of arc, and in median vertical section 45° of arc. Genal spine extends back to the pygidium, is only slightly curved, and has a pair of posterodorsally directed spines on its dorsal surface. Doublure on anterior part of free cheek is almost vertical beneath the marginal spines and is turned up abruptly inside. The vertical portion diminishes toward the back, so that at the base of the genal spine it has almost disappeared. Vertical part is covered with fine granules; remainder is smooth. There is a small antennular notch just outside the connective suture. Rostral plate is transverse; rostral suture measures almost twice the width (tr.) of the hypostomal suture; anterior edge of rostral plate is slightly sinuous and posterior edge is broadly concave; surface is covered with fine granules but has a slightly enlarged row of granules close to the anterior edge behind a faint furrow that borders the rostral suture.

Thorax has 8 or 9 segments. Two or 3 tubercles of variable size are present on each side of the first 2 or 3 axial rings, and 1 or 2 on the more posterior segments; the adaxial tubercles are the largest, and the abaxial the smallest; a median tubercle is present on the 1st segment on some specimens. A single large tubercle is present on the principal band of each segment, just adaxial of the fulcrum; otherwise all surfaces are smooth and without granulation. Posterior pleural spine on the 3d segment is the longest and thickest on whole thorax; spine on 4th segment is very much smaller in diameter and only about half as long as that on the 3d. Spines on 5th and later segments are intermediate in diameter between those on 3d and 4th. All posterior spines turn down a little at the fulcrum and then curve up distally, the amount of curvature increasing progressively on the more posterior segments. Anterior spines on 4th and more posterior segments have trifid tips and a small anterior projection lateral to the fulcrum; the 3d segment has a short, simple anterior spine extending laterally from this anterior projection; the first 2 segments have a small, downturned flange.

Anterolateral corner of pygidium is distinctly truncated. Axial furrow is weak opposite the first segment, deep posterior to this, but almost disappears axially. Axis of pygidium has a clearly defined and complete anterior ring, with 1 or 2 tubercles on each side; 2d ring has a well-defined pseudo-half ring, is arcuate in shape, swollen laterally, and has 1, or rarely 2, tubercles on each side of the median line. A vestigial third ring is represented by a small medial eminence crowned by a tubercle. Posterior pleural band of anterior segment extends back into the dominant marginal spine; it is incomplete on all specimens, but probably was about equal in length to the axial length of the pygidium; it is distinctly curved posterodorsally. Three spines are present lateral to the principal spine, the most anterior of the three showing a bifid tip on well-preserved individuals. Only one pair of spines is present between the principal pair, and these are a little shorter and thinner than the first lateral. There is one tubercle only on the principal pleural ridge just in front of the base of the spine. Up to four small tubercles can be seen on the anterolateral corners of the anterior pleural band of the first segment but none on the bases of the spines connected with this unit. Dorsal surface of the pygidium has no granulation. Doublure is narrowest anteriorly, widens slightly backward and has a rather steep inner face; outer part is moderately to strongly convex and is covered with fine granules. Ventral surface of marginal spines is also granulose.

Description of Type B.—This differs from Type A in the following features:

1. The posteromedian tubercle on the occipital ring and the tubercles surrounding it are larger.
2. There are tubercles all over glabellar lobe 1p.
3. Tubercles cover the entire surface of the free cheek, including the border furrows, and they are much denser on the lateral border than in Type A.
4. The border spines on the cheeks are marginally longer.
5. The pair of tubercles down the thoracic pleurae is invariable. Also, there are several much smaller tubercles on some of the thoracic posterior pleural spines lateral to the fulcra. Two specimens (see Whittington, 1956a, pl. 58, fig. 2) have a tubercle on the *anterior* pleural band of the last segment.
6. The pygidium usually has 2 tubercles on the posterior pleural band of the 1st segment, 1 tubercle at the base of each of the marginal spines medial and lateral to the principal spine, and 3 or 4 tubercles in the anterolateral corners of the pygidium.
7. There are 2 spines on each side of the 1st pygidial axial ring, and up to 5 on the 3d ring.
8. All specimens have eight thoracic segments.

Hypostomes.—One Type A hypostome has been found in place. In addition, there are three isolated specimens: the one figured by Whittington (1956b, pl. 57, fig. 16), another in the collections of the Smithsonian Institution, and a third in the American Museum of Natural History. Photographs of the latter have been sent to me by Dr. Niles Eldredge. I cannot see any morphological differences between the specimens. It is not known if they belong to Type A only or to both morphs. The description is as follows:

Outline is subquadrate, almost square. Anterior margin is broadly convex; lateral margin is slightly sinuate and has a distinct but extremely small marginal projection in the posterolateral corner. Posterior margin is almost straight medially. Border furrow is continuous round the entire hypostome but almost disappears anteromedially. Lateral border is highly convex, posterior border rather flatter, and anterior border an almost flat flange. Posterior border turns dorsad medially. Middle body is flatly convex. Middle furrow is short, deep, posteromedially directed, and is situated almost one-third of the total length from the anterior margin. In the corner of the posterior lobe directly behind the middle furrow is a tiny, elevated, circular macula. Four or five flat tubercles lie in the anterolateral corner of the anterior lobe, none being represented by a definite pit on the inner surface of the hypostome. Whole surface is covered with densely packed, fine granules. Anterior wings are strong and are anterolaterally directed. Posterior wing is situated two-thirds of the length back from the anterior edge and is flat-triangular in shape. Doublure in position of lateral notch is rather flattened; elsewhere almost vertical. Internal surface has pits arranged in a definite pattern: a large crescentic pit lies in the anterolateral corner of the middle body and on the adjacent furrows, posterior to which is the pit corresponding with the macula on the ventral surface; 10-12 pits arranged to form a peltate outline with its broad curved anterior edge just inside the anterior border furrow, and its posterior edge formed by a pair of large shallow pits a little behind the midpoint of the hypostome. This group of pits outlines the flattened median part of the anterior lobe of the middle body.

These pits are quite different from those on other species of *Leonaspis*. The specimens figured by Chatterton (1971, pl. 9, figs. 3, 5, 6, 15) show the external tuberculation of the middle body, but the pits on the internal surface are finer and more numerous, and the larger anterolateral pits (if they are present at all) lie within the corners of the middle body. Those figured by Whittington and Campbell (1967, pl. 16, figs. 16-18) seem to have no pitting on the internal surface.

Remarks.—In erecting this species, Whittington commented that it was very similar to *L. tuberculata* (Hall) from the Helderbergian of New York, the main differences being that *williamsi* had a short occipital spine and 8 rather than 9 thoracic segments. The latter point is now known to be inaccurate, but the former remains valid. However, examination of a collection from the New Scotland Formation at Clarksville, New York, has convinced me that *L. tuberculata* is in need of revision. The following points need to be made with respect to the description and figures given by Whittington (1956b):

1. Many specimens have larger and more closely spaced turbercles on the cranidium than are shown on Whittington's plate 57, figures 1-3.
2. There is a fine granulation on and between these tubercles and on the occipital spine.
3. The anterior border on some specimens is almost flat and preglabellar furrow is weak.
4. The genal spines are strongly curved inward toward their extremities. They have up to four spines on their inner dorsal edge, the proximal one being quite short.
5. At least some of the free cheeks have a group of tubercles up under the eye, and between that and the border there is a series of irregular radiating caecal ridges. These cross the border furrow.
6. There seem to be 13 or 14 marginal spines on the cheek. The proximal ones are faintly club shaped, and the distal ones are very long and slender.
7. The hypostome has the middle furrows meeting the border furrows well forward of the midlength, deep laterally, but showing an almost indistinguishable continuation right across the median body. The whole ventral hypostomal surface is granulate, and in addition the anterior border and the anterior lobe of the median body have irregular "tubercles" that represent the external expression of the muscle insertions on the dorsal face.
8. Some specimens have a single tubercle on the principal band of the thoracic segment, and this is at the fulcral end. Such specimens do not have tubercles on the anterior pleural ridge.
9. The axial rings of the thorax are tuberculate. The tubercle on either side of the midline is the largest, and there is a small median tubercle and a group of 3 or 4 others of similar size on the flanks.

With the new information of the tuberculation of the thorax, it is possible that this species, like *L. williamsi,* is dimorphic. This possibility needs further investigation.

There is now a formidable list of features by which *L. tuberculata* may be distinguished from *L. williamsi.* Both morphs of *L. williamsi* have shorter and straighter genal spines with fewer spines on their inner dorsal edge; weaker tubercles on the cranidium; more club-shaped marginal cephalic spines; different tubercle patterns in the axial rings of the thorax; less curved principal spines on the thorax; and longer median paired spines on the posterior of the pygidium.

In addition to these differences, there are others that are peculiar to each morph. These are related to tuberculation of the free cheeks. However, despite these differences, it remains true that *williamsi* is closer to *tuberculata* than to any other species described.

Also, in the light of the new data, the species described as *L. tuberculata favonia* by Haas (1969) from the Wenban Limestone of Nevada is seen to be just as close to *L. williamsi* as to *L. tuberculata,* and the figured specimens of *L.* cf. *williamsi* of Whittington and Campbell (1967) are seen to be quite close to *L. williamsi* of Type B.

Bruton (1967, p. 227) commented on a similarity between *L. crenata* (Emmrich) from the Wenlockian Mulde Beds of Gotland and *L. williamsi,* pointing out especially the similarity in the free cheek, occipital spine, and pygidium, though noting also the differences in ornament and the hypostome. The similarities certainly are there, but without intermediates it is not possible to speculate on relationships.

Material.—Only the best preserved specimens are listed.

Type A.—OU 5273, ANU 14898, 21889, 21895, 21903, 21906, 21908, all from the Haragan Formation at Old Hunton Townsite, NW¼ sec. 8, T. 1 S., R. 8 E., Coal County; OU 6529 from the Haragan Formation at White Mound, NW¼NE¼ sec. 20, T. 2 S., R. 3 E., Murray County.

Type B.—OU 5276-78, OU 6530a-e, all from the Haragan Formation at White Mound. OU 6531a-b and OU 4250a-b labeled "Arbuckles;" ANU 21897, 21899, 21907, from Old Hunton Townsite.

Intermediate.—OU 5276b and OU 6532, from White Mound; ANU 21891, from Old Hunton Townsite.

Family MIRASPIDIDAE Richter and Richter 1917

Subfamily MIRASPIDINAE Richter and Richter, 1917

Remarks.—Prantl and Přibyl (1949) were impressed by the similarity of the cephalon of their genus *Ceratonurus* to that of

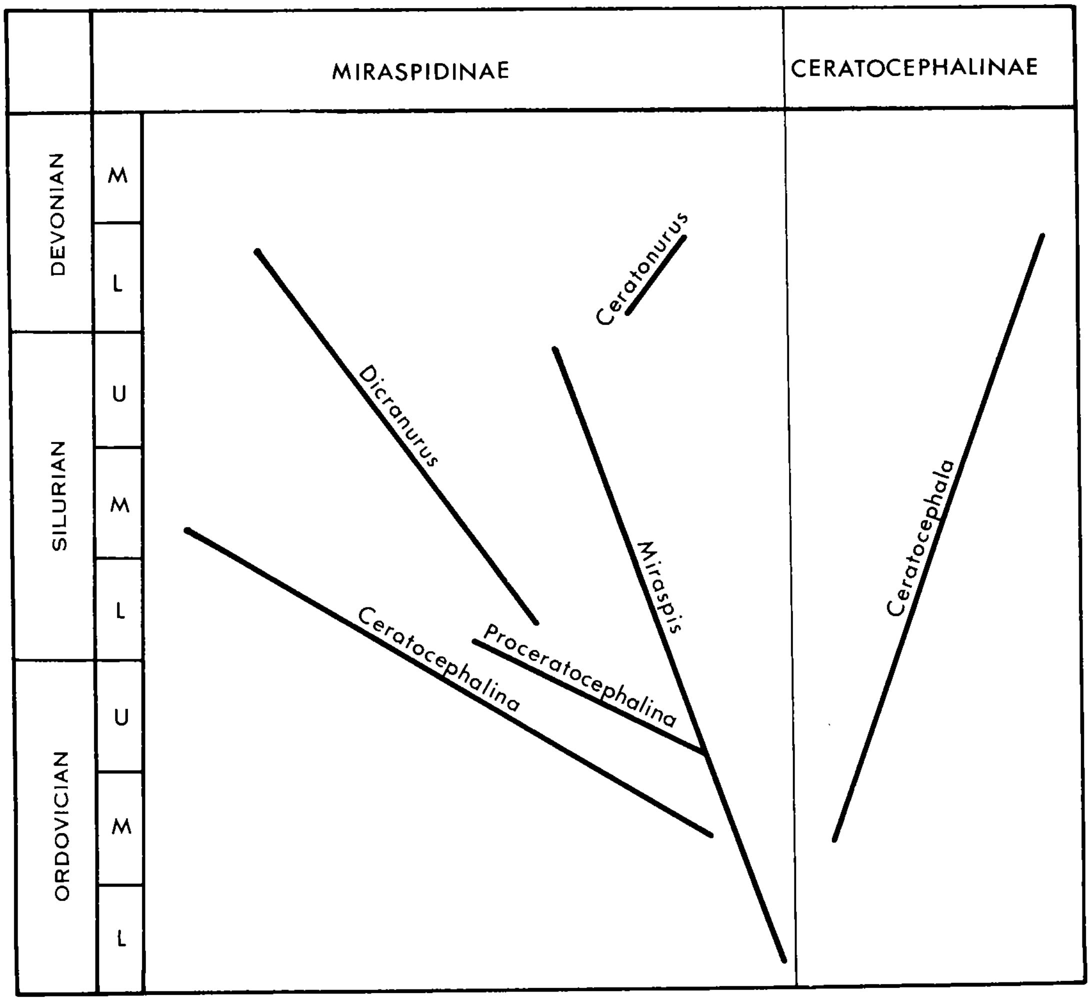
Ceratocephala Warden, the thorax to that of *Dicranurus* Conrad, and the pygidium to that of *Miraspis* Richter and Richter. Nevertheless they assessed the relationship with *Dicranurus* as the strongest and expressed this conclusion by placing *Ceratonurus* and *Dicranurus* in a separate Subfamily Dicranurinae within the Family Ceratocephalidae. Subsequent workers, e.g., Whittington (1956a) and Bruton (1968), have not accepted this but have preferred to associate all four genera (together with others) in the Subfamily Miraspinae. Bruton, however, concluded that *Ceratonurus* is more likely to be related to *Miraspis* than to *Ceratocephala,* a view with which I am in agreement. In addition to the reasons advanced by Bruton, it is now known that the free cheeks of *Miraspis* and *Ceratonurus* are similar in gross form and in the shape and disposition of the fringing spines. The thoracic segments of the 2 genera are similar not only in gross features, such as the shapes of the pleural bands and ridges, but also in such minor features as the similarly shaped and barbed anterior pleural spines and the presence of a 3d spine between the anterior and principal pleural spines (but not on the 8th segment). I suspect that, although Bruton records anterior spines on all segments of *Miraspis mira,* the spine is either absent or atrophied on the ninth segment, as it is in the Haragan species of *Ceratonurus*. Also, whereas the posterior spines of the first 7 segments are smooth, those of the 8th and 9th segments are barbed in both genera. Finally, their pygidia are remarkably similar in both segmentation and spine pattern. All these detailed similarities argue strongly in favour of phyletic relationship.

The relationships of *Dicranurus* are not so clear. As is shown below, the species can be traced back to the Early Silurian, and so its origin must be in a group of that age or older. There is a certain similarity to *Ceratocephala,* particularly in the form of the hypostome, but the differences in the definition and shape of the glabellar lobes, the structure of the thoracic pleural bands, and the axis and marginal spines of the pygidium indicate that the two genera are not closely related. It is easier to see similarities in glabellar lobation and thoracic pleural structure between *Dicranurus* and *Miraspis,* although *Dicranurus* lacks the third spine on the thoracic pleural tips. *Dicranurus* also has a transverse rather than a subtriangular hypostome. It seems likely that *Dicranurus* was derived from a *Miraspis*-like form that had reduced the marginal spines on the cheeks and pygidium by the Late Ordovician or Early Silurian. The only known candidates for relation to *Dicranurus* are *Proceratocephala* Prantl and Přibyl and *Ceratocephalina* Whittington, both of which are more closely allied to *Miraspis* than to *Ceratocephala* (see Whittington, 1956b; Bruton, 1968). *Whittingtonia* Prantl and Přibyl, 1949, a Late Ordovician genus that is commonly placed in the Miraspidinae, has so little in common with the other members of the subfamily that I consider that it should be regarded as *incertae sedis*.

Both *Proceratocephala* and *Ceratocephalina* have pygidia that tend toward the subtriangular form shown by *Dicranurus,* but *Ceratocephalina* is peculiar in the breadth of the median lobe of its glabella and occipital ring and in the development of the median occipital spine, *Proceratocephala,* on the other hand, has a glabellar morphology similar to that of *Dicranurus,* and judging from the figures of *P. terribilis* (Reed) given by Whittington (1956b, pl. 60, figs. 2, 5), the marginal spines of the free cheeks are reduced in length by a process of fusion of their bases. I draw this conclusion from the unusual width of the border. It is significant that *Dicranurus* also has an unusually wide border with a correspondingly wide doublure, suggesting that it has lost its spines by progressive fusion at their bases. *Dicranurus* probably arose early in the Silurian from a *Proceratocephala*-like animal.

It seems certain, therefore, that:

1. *Dicranurus* and *Ceratonurus* had separate evolutionary origins in the same basic stock, and the Dicranurinae of Prantl and Přibyl is not a natural group.
2. The genera *Miraspis, Proceratocephala, Ceratocephalina, Dicranurus,* and *Ceratonurus* form a fairly compact group characterized by the deep dorsal and longitudinal glabellar furrows; well-rounded lateral glabellar lobes; a strong principal pleural band and weaker, but clear, anterior and posterior bands on the thorax; and one major pair of marginal spines on the pygidium.



Text-figure 31. Phylogenetic relationships of genera and subfamilies of Family Miraspididae Richter and Richter.

3. *Ceratocephala,* with its poorly defined holaspid glabella, unique thoracic pleurae, and pygidium with several major, barbed marginal spines, must have separated from the root stock by the Early Ordovician (Bruton, 1966, p. 25). This genus seems to be sufficiently distinct to warrant recognition as a separate subfamily. I have no views on *Koneprusia* Prantl and Přibyl or *Isoprusia* Bruton except that they cannot be regarded as close relatives of *Dicranurus.*

4. I therefore propose to recognize the Miraspidinae Richter and Richter for the genera indicated in 2 above, and the Ceratocephalinae for *Ceratocephala* (with the possible addition of other genera). These would then be united to form the Family Miraspididae Richter and Richter, 1917.

Since the above was written, the paper by Přibyl and Vaněk (1973) has come to hand. It attempts a classification of the odontopleurids based on hypostomal characters and has come to significantly different conclusions from mine. In particular, (a) *Miraspis, Ceratocephala,* and *Ceratonurus* are regarded as closely related and as members of the *Miraspidinae;* (b) *Dicranurus, Koneprusia,* and *Isoprusia* are retained as members of the *Dicranurinae;* and (c) *Certaocephalina* is considered to be a possible intermediate between the Miraspidinae and the Apianurinae. There is certainly considerable similarity between the newly figured hypostome of *Ceratonurus* and *Ceratocephala,* but this does not demonstrate the proposed relationship of these two genera, nor the relationship of either with *Miraspis.* These hypostomes have as much in common with *Selenopleura* as with *Miraspis.* Further, the hypostome of *Dicranurus* also has considerable similarity to that of *Ceratonurus* but very little in common with those of *Koneprusia* or *Isoprusia,* with which Přibyl and Vaněk would classify it on other grounds. At present, I see no reason to conclude that hypostomes are more reliable guides to relationships than are features of the dorsal exoskeleton.

Genus **Ceratonurus** Prantl and Přibyl, 1949

Type species.—Acidaspis krejcii Novák from the Dvorce-Prokop Limestones of Bohemia (Pragian).

Remarks.—This genus is poorly understood because of the lack of good material, both of the type species and the only other species previously assigned to it with confidence, namely *C. selcanus* (Roemer) from the Lower Devonian of Germany (see Bruton, 1968, for discussion). The hypostome has remained inadequately described (Prantl and Přibyl, 1949, p. 191); there has been confusion about the association of cephalon and pygidium; and the thorax, which was known to Novák, who described its general features, could not be found by Bruton (1968, p. 53).

If we accept the assignment of the Oklahoma material to the genus (for argument see below), it is possible to add the following features to the diagnosis given by Bruton:

Occipital ring has a narrow but distinct posterior band; free cheeks have numerous anteroventrally directed fringing spines. Thoracic segments have powerful principal and weaker anterior pleural ridges, and a narrow posterior pleural band; principal pleural spines are present on all segments; anterior pleural spines are compressed and have barbed edges; there is a stunted 3d spine between the anterior and posterior pleural spines on some segments (not the 8th). The pygidium is with or without marginal spines lateral to the major pair.

Ceratonurus, new species

Pl. 37, figs. 1, 2

Miraspis sp. undet. Whittington, 1956b, p. 515.
"Ceratonurus," sp. undet. Ormiston, 1968, p. 1196, pl. 158, fig. 12.

Description.—Cephalon is rather crushed; length (exclusive of genal spines) is estimated to be 0.6 times width; strongly convex. Glabella is differentiated by weak axial furrows that become broad and much less definite at the occipital ring; occipital furrow is slight and is situated well forward medially (one-third of the distance along lobe 1p) swinging back and becoming very deep behind 1p, shallowing again to the axial furrow; a pair of strong spines is developed from the anterior part of the ring, length unknown; posterior band is well defined, rather flattened, of uniform length (exsag.) behind the median glabellar lobe but tapers to a point laterally; small tubercles are present between and in front of occipital spines. Median glabellar lobe is long, narrow, and parallel sided; relation to anterior border was not observed; arrangement of tubercles is not certain, but there were probably six pairs of slightly enlarged tubercles symmetrically placed along the crest of the lobe, with another one between the most posterior pair; smaller tubercles are irregularly scattered. Lobe 1p is more or less ovate, but with its adaxial edge rather straight; two irregular rows of slightly enlarged tubercles are arranged lengthwise along it, with smaller tubercles scattered between. Furrow 1p forms a pit against the median furrow, becoming very shallow laterally. Lobe 2p is subtriangular and bears 4 or 5 slightly enlarged tubercles and a few smaller ones. Furrow 2p is similar in type to 1p. Lobe 3p is obscure, owing to fracture.

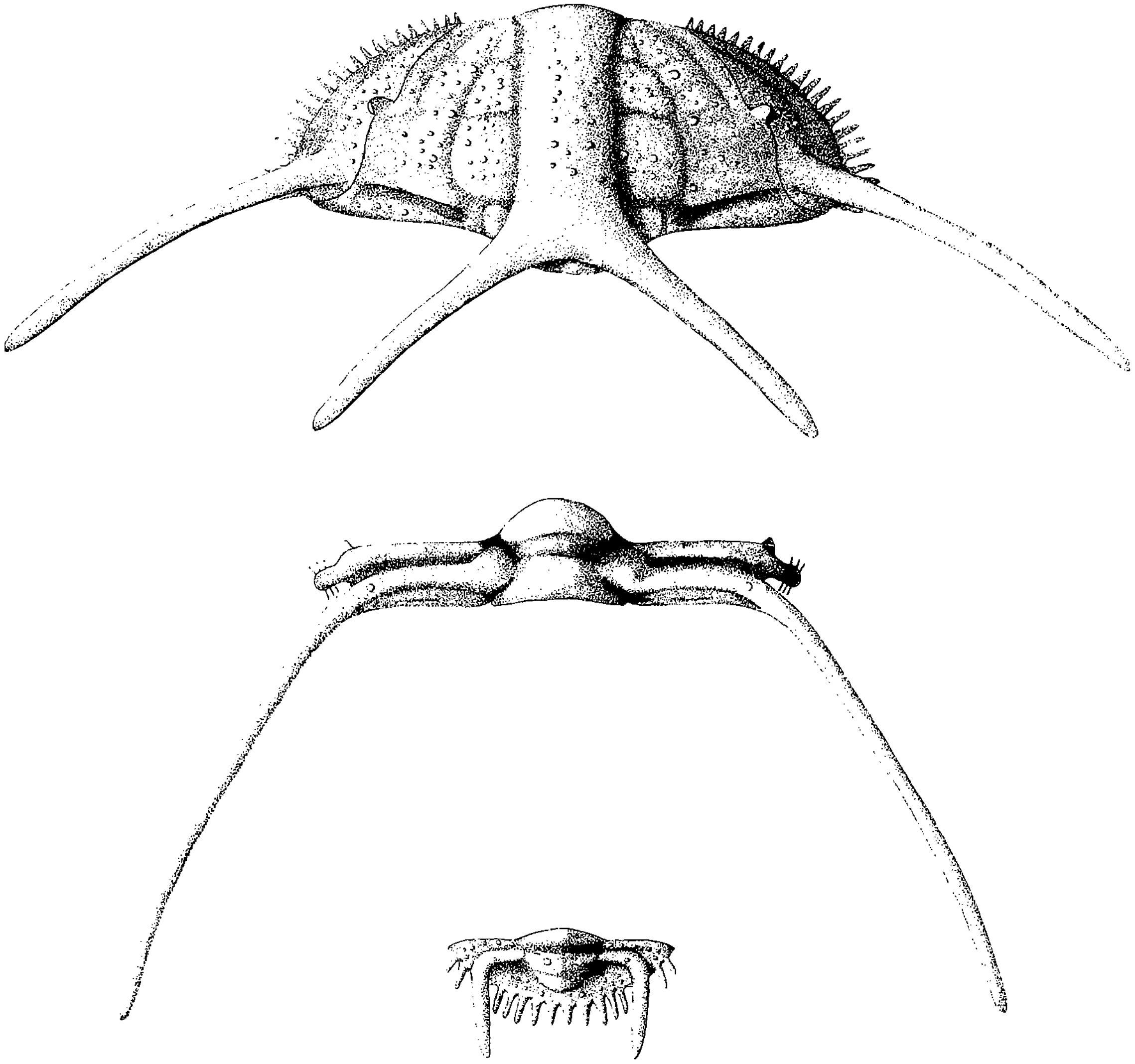
Fixed cheek is strongly arched longitudinally; posterior border furrow fades abruptly at the axial furrow; posterior border trebles its length (exsag.) between the axial furrow and the genal spine; palpebral lobe is short, apparently only moderately upturned, and is situated in line with the anterior end of lobe 1p; eye ridge is slight, straight. Facial suture runs back slightly obliquely from the palpebral lobe to inside the base of the genal spine, and in front of the eye it runs anteromedially, diverging only slightly from the eye ridge; anterior end of facial suture and rostral suture were not observed. A row of 4 strong tubercles is present just outside the axial furrow; 4 or 5 rather smaller tubercles lie along the eye ridge, and a few irregular ones behind the palpebral lobe; still smaller ones are distributed irregularly.

Free cheek has a prominent, almost straight genal spine directed posterolaterally and a little upward; base of spine continues around cheek, forming a prominent ridge that fades away in front of the palpebral lobes; eye surmounts a prominent pedicel of unknown height; the 15 or more short, needlelike marginal spines present are ventrolaterally directed, the longest posteriorly, and diminishing progressively anteriorly; 2 rows of slightly enlarged tubercles lie along the border; smaller ones are irregular.

Thorax is long and narrow with 9 segments; axis is highly arched; articulating half ring measures about 0.6 times the length (sag.) of the remainder of the ring; articulating furrow is long and shallow, transverse across the crest but inclined forward down into the axial furrows; median band of ring slopes into articulating furrow at about 45° and is well rounded on top; posterior band is about the same length as the median band, is much flatter, and lies at a slightly lower level; a prominent tubercle is present on each side of the midline on each median band; much smaller tubercles and granules are scattered over the ring, particularly the posterior band. Each pleura has a pronounced principal ridge, well rounded, and forming by far the highest part; anterior band is well developed on all pleurae, well rounded on its crest, decreases in length (exsag.) abruptly toward the axial furrow, and increases slightly beyond the fulcrum; on all segments posterior band is flatter and shorter (exsag.) than either of the other bands, very short on 1st segment, increasing to a maximum of about one-quarter the total pleural length on the 5th and then reducing progressively to almost nil on the final segment; all posterior bands are lanceolate in outline. A small but distinct tubercle is present on each principal pleural ridge at about the line of the fulcrum, and a similar tubercle, or pair of tubercles lies near the middle of each anterior band.

Anterior pleural spine is not present on 1st segment, is short and posteroventrally directed on the 2d, increases gradually in length and also becomes a little more laterally directed back to the 6th segment; on 7th and 8th segments spine is about the same length as on 6th but is more posteriorly directed; spine of 9th segment is reduced to a tiny stub; all spines are rather compressed and have a single row of barbs along anterior and posterior edges. Posterior pleural spine on 1st segment is a little narrower (tr.) than the width of the pleura and is curved downward, outward, and forward beneath the genal spine; posterior spine on 2d segment (broken at tip) measures at least 1.5 times the pleural width, is distinctly flexed in a sigmoidal fashion in dorsal view, but also turns down slightly proximally and up distally; spine on 3d segment is broken, but it probably was at least the size of the 2d one, straight, and directed almost transversely; 4th, 5th, and 6th spines are incomplete but obviously were along and progressively more posteriorly directed, the 5th also being slightly arched upward; 7th, 8th, and 9th spines diminish abruptly and progressively in length and diameter, and all posteriorly are directed or slightly curved inward. Between the posterior and anterior spines and a little ventrad to them, at least on segments 5 to 7, there is a small tubercle-like median spine (pl. 37, fig. 2d); 8th segment has no such spine, but 9th segment has a much enlarged one, dominating the reduced anterior spine. End of pleura (below the spine bases) is squared off and has slight projections at the anterior and posterior ends; anterior spine articulates into cavity between the posterior projection and the posterior spine of the preceding segment during enrollment; anterior projection fits inside posterior projection of the preceding segment. Granules and small tubercles are common toward the pleural tips, especially on the anterior bands and on the bases of the spines.

Pygidium is small and is approximately equal in width to the occipital ring; axial furrow is weak, especially posteriorly; 1st axial ring is short and has a pair of tubercles like those of the thorax; 2d axial ring is very



Text-figure 32. Reconstructed cephalon, thoracic segment, and pygidium of *Ceratonurus* sp. from Haragan Formation.

poorly defined and has a vague pseudo-half ring; principal pleural band of 1st segment is low, proximally more or less at right angles to the axis, and distally turned back sharply into the slightly recurved principal border spine; there are 5 small border spines medial to the principal one, and 2 lateral to it, on each side of the axis; scattered small tubercles are present on the pleural regions and on the 2d axial ring; a slightly enlarged tubercle lies on the principal pleural band adaxial of the spine base; principal pleural spine is definitely barbed; smaller border spines have faint barbs; doublure is directed inward beneath the spines and then turns upward sharply, forming a sharp carina; at least the outer part is granulate.

Remarks.—The comments on the structure of the median (3d) spines on the pleural tips are based on the specimen with only segments 5 to 9 preserved. It is not implied that such spines are absent on the preceding segments; they have just not been observed.

The more nearly complete of the two specimens on which the description is based was first described by Whittington (1956b) as *Miraspis* sp. Bruton (1968) already pointed out that the forward position of the eye lobe suggests a relation to *Ceratonurus,* though it should be noted that in both *C. krejcii* and *C. selcanus* the eye is even farther forward than in the Oklahoma species. The extremely stunted nature of the third spine on the thoracic pleural tips and the shape and orientation of the anterior pleural spines also differentiate this form from *Miraspis*. Owing to lack of information on these structures in European species of *Ceratonurus,* no sure conclusions can be drawn about their significance, but the figures given by Novák (1883, pl. 10, figs. 15a-c) suggest that in *C. krejcii* the third spine is small or absent and that the anterior spine is downturned as in the Oklahoma species. Finally, the size of the axis of the pygidium is closer to that of *C. krejcii* than to species of *Miraspis*. It is probable, therefore, that Bruton's suggested assignment of the Oklahoma specimen to *Ceratonurus* is correct.

In addition to the more anterior position of the eye, our specimen can be distinguished from *C. krejcii* by the more anteriorly placed occipital spines, finer cephalic tubercles, less transverse pygidium, and fewer pygidial marginal spines. *C. selcanus* has much coarser cephalic tubercles, more posteriorly placed occipital spines, and deeper axial and glabellar furrows.

Material.—ANU 21900, from the Haragan Formation at Old Hunton Townsite, NW¼ sec. 8, T. 1 S., R. 8 E., Pontotoc County. The specimen figured by Whittington (1956b) is from the Haragan Formation at White Mound, SE¼ sec. 20, T. 2 S., R. 3 E., Murray County.

Genus **Dicranurus** Conrad, 1841

Type species.—*Acidaspis hamata* Hall, 1859, from the New Scotland Formation (Lower Devonian), New York.

Remarks.—This genus includes the American type species; the European, North African, and Central Asian *D. monstrosus* (Barrande); and the Australian *D. longispinus* (Mitchell) and *D. kinglakensis* Gill. In addition, *D. gracilicauda* Erben, *Orphanaspis orphanus* (Barrande), *Selenopeltoides hawlei* (Barrande), all of which are very poorly understood from pygidia only (see Bruton, 1968, p. 59), may belong to the genus. Recent discussions of the generic diagnosis are given by Bruton (1968) and Maksimova (1968). It is worth noting that, despite the emphasis on the structure of the dorsal exoskeleton of the cephalon and the pygidium (parts that are most commonly preserved), the thorax in all the above species has features that are of equal diagnostic value. It is unfortunate that the only attempt to use the thorax for diagnostic purposes (Whittington, 1956a) is inaccurate because it was based on inadequate material. This, together with the recent discovery of a hypostome, makes a new diagnosis desirable.

Most workers have agreed that members of the Odontopleuracea have 2 or 3 lateral glabellar furrows. In some genera, however, the median glabellar lobe extends anteriorly to form a lobe in front of lobe 3p. Examples of genera displaying this structure are *Miraspis* (Bruton, 1968, pl. 7, figs. 4-7), *Primaspis* (Whittington, 1956b, pl. 1, figs. 1, 2), *Dudleyaspis* (Campbell, 1967, pl. 19, figs. 5, 6), and the present genus. This feature has not been regarded as a lateral glabellar lobe but as a "swollen lateral expansion of the frontal lobe" that joins the eye ridge (Bruton, 1968, p. 44) or simply as part of the eye ridge itself. Examination of the figures listed above and of the *D. hamatus* described herein demonstrates that (a) although the axial furrow is usually very weak, it can often be seen bounding this lobe laterally; (b) it is separated from the median lobe by a change in slope, if not a furrow; (c) although it lies directly opposite the eye ridge in some genera, it is distinctly offset in others. In view of these points it seems reasonable to regard the expansion as a fourth glabellar lobe, and this has been done in the ensuing text.

This is the first time that the hypostome of *Dicranurus* has been described. Examination of the types of *D. longispinus,* however, shows a relatively well-preserved external mold of a hypostome on F 2771b Australian Museum Collections. This mold is identical in form, furrows, and pits with that of *D. hamatus elegantus*. The Australian species also has a poorly preserved rostral plate of rodlike shape.

Diagnosis.—Cephalon is transverse in outline; there are a long median glabellar lobe and four lateral lobes, the most anterior being an expansion of the median lobe; occipital ring has a very narrow posterior band which is incomplete medially; there is a pair of strong, hooked occipital spines; genal spines are dorsolaterally directed and are derived from well up on the cheeks; no border spines are present on free cheeks; eye stands on a pedicel and is placed opposite the anterior part of lobe 1p. Cephalic ornament consists of scattered low tubercles and a fine, dense granulation. Hypostome is very transverse and has a pair of depressions in the anterolateral corners of the middle body, a broad posterior embayment, and a vertical posterior doublure. Thorax has 9 segments, each with a high, well-rounded principal pleural ridge, a low anterior ridge, and a narrow posterior area; principal pleural spines are strong, the 4th being greatly enlarged and the 5th greatly reduced; anterior pleural spines are low, bladelike, ventrolaterally directed, and expanded at their ventral tips. Pygidium has two axial rings; a single strong pleural ridge extends back into a pair of strong spines; no accessory spines are present.

Range.—The oldest described species that can be definitely assigned to the genus is *D. longispinus* (Mitchell), which is reported from the Middle and Upper Trilobite Beds, Bowning, New South Wales. The former unit is of uppermost Ludlovian age (Jaeger, 1967; Link, 1970). Mr. L. Sherwin, of the Geological Survey of New South Wales, has shown me an undescribed specimen of the genus from the late Llandovery Boree Creek Formation of central New South Wales (Sherwin, 1971b, p. 210), and Bruton (1968, p. 59-60) believes that the Wenlockian specimens described as *Acidaspis hawlei* Barrande from Bohemia are valid members of the genus. The youngest species is *D. monstrosus* from the Pragian.

Dicranurus hamatus elegantus, new subspecies

Pl. 34, fig. 7; pl. 35, figs. 2-3; pl. 36, figs. 1-5

Dicranurus hamatus (Hall); WHITTINGTON, 1956b, p. 518, pl. 60, figs. 9, 11-15.

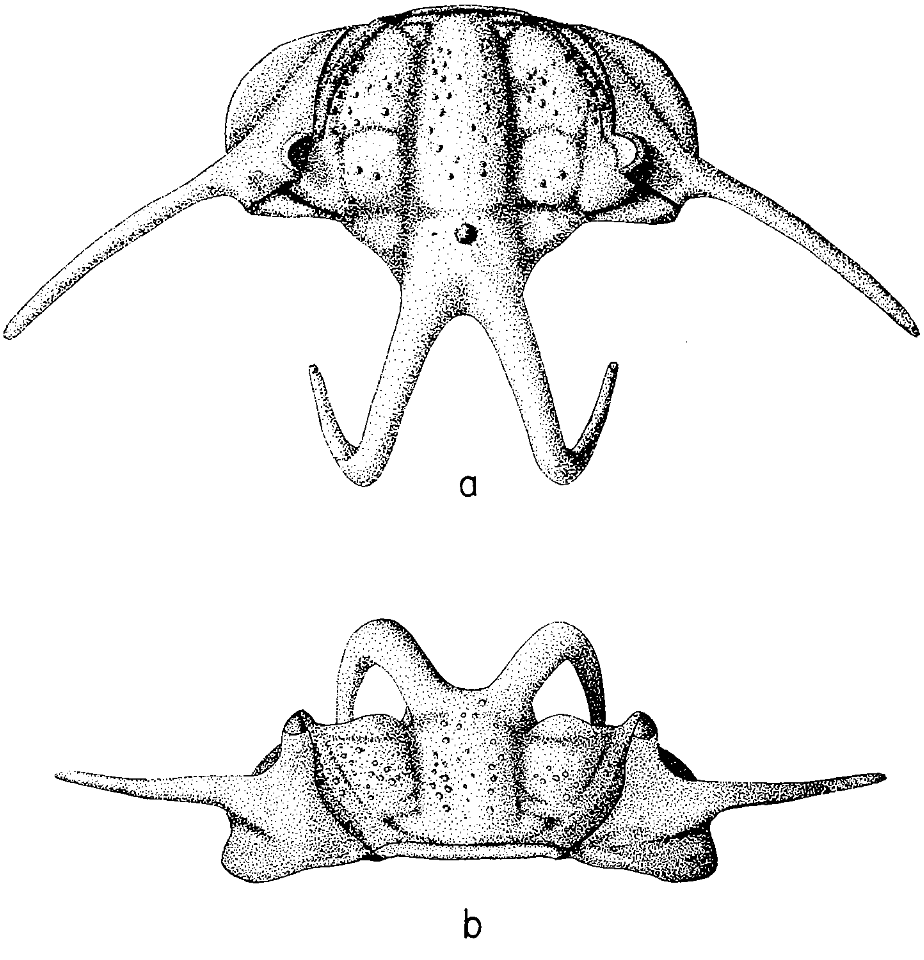
Types.—Holotype: OU 5275 from the Haragan Formation, Old Hunton Townsite, NW¼ sec. 8, T. 1 S., R. 8 E., Pontotoc County (near base of section by the old barn). Paratypes: OU 3249, OU 5281-82, and OU 6540 also from the Haragan Formation at Old Hunton Townsite; OU 5280 and OU 5283 from the Hunton Formation at White Mound.

Diagnosis.—Like *D. hamatus hamatus* but with more slender occipital spines and a less massive occipital ring at the holaspid stage, weaker tubercles on the cranidium, more delicate palpebral lobes, and a narrower median glabellar lobe.

Description.—Cephalon is delicately constructed. Median lobe of glabella expands slightly to the rear, is broadly rounded to subquadrate in front; longitudinal furrow is broad and deep over almost its entire length, but suddenly diminishes before reaching the anterior furrow; axial furrow is not distinguishable lateral to the occipital ring; it is broad and very shallow inside the palpebral lobes, then gradually fades away to the front of lobe 2p, where it almost disappears before deepening slightly into the anterior furrow; occipital ring is strongly triangular in outline; median lobe of occipital ring broadens posteriorly a little more abruptly than the remainder of the median glabellar lobe and is highly arched; occipital spines are recurved through about 200°; their distal ends are blunt and only moderately deflected laterally, so that they lie approximately on an exsagittal line through the palpebral lobes; lateral occipital lobes are very much lower than the median lobe, markedly triangular in dorsal aspect, slightly peaked dorsally but curve around to form a posterior surface on which a posterior band is clearly differentiated; this posterior band is absent or scarcely visible beneath the bases of the occipital pines; occipital furrow is long (sag., exsag.) and shallow across the median lobe, deeper and much shorter lateral to the longitudinal furrow, then fades abruptly to the axial furrow; glabellar lobe 1p is moderately inflated, but not as high as the median lobe, ovate in outline, and weakly but clearly defined in front by furrow 1p, which is convex forward; lobe 2p is more elongate but lower than 1p and narrows slightly forward; furrow 2p is weak and also convex forward; lobe 3p is minute, transverse, and raised only slightly above the surrounding furrows; on well-preserved specimens an anterior lobe about the same size as 3p extends laterally from the median lobe to produce a "hammer-head" type of structure (pl. 35, figs. 2b, 3c); anterior border furrow is shallow medially, deepening markedly lateral to the axial furrow; anterior border is very short (almost linear) medially, but becomes 3 or 4 times longer (exsag.) laterally.

Palpebral lobe is approximately two-thirds as long as lobe 1p, is almost semicircular in outline, and has δ situated a little forward of the middle of lobe 1p; palpebral lobe is deflected up from the very weak palpebral furrow at about 35° in anterior profile, but its distal extremity arches down toward the horizontal; eye ridge is prominent and is clearly defined by a sharp break in slope on both its flanks, it is almost straight posteriorly but curves axially anteriorly, where it disappears into the anterior furrow; fixed cheek is quite steep posterior to the palpebral lobe; posterior border furrow is narrowest adaxially, is not joined to the occipital furrow, and becomes deeper and longer (exsag.) laterally; posterior border is strongly convex and bears a shallow groove along its posterior edge to produce what appears to be a narrow articulatory flange adaxial to the fulcrum.

Facial suture diverges at about 10° from the eye ridge in front of the palpebral lobe, β is broadly rounded, and at α makes a markedly angular junction with the anterior margin; posterior to the palpebral lobe it



Text-figure 33. Reconstruction of dorsal (*a*) and anterior (*b*) views of cephalon of *Dicranurus hamatus elegantus,* new subspecies, from Haragan Formation.

drops almost vertically to the border furrow and then runs a course at about 35° to the posterior margin to ω.

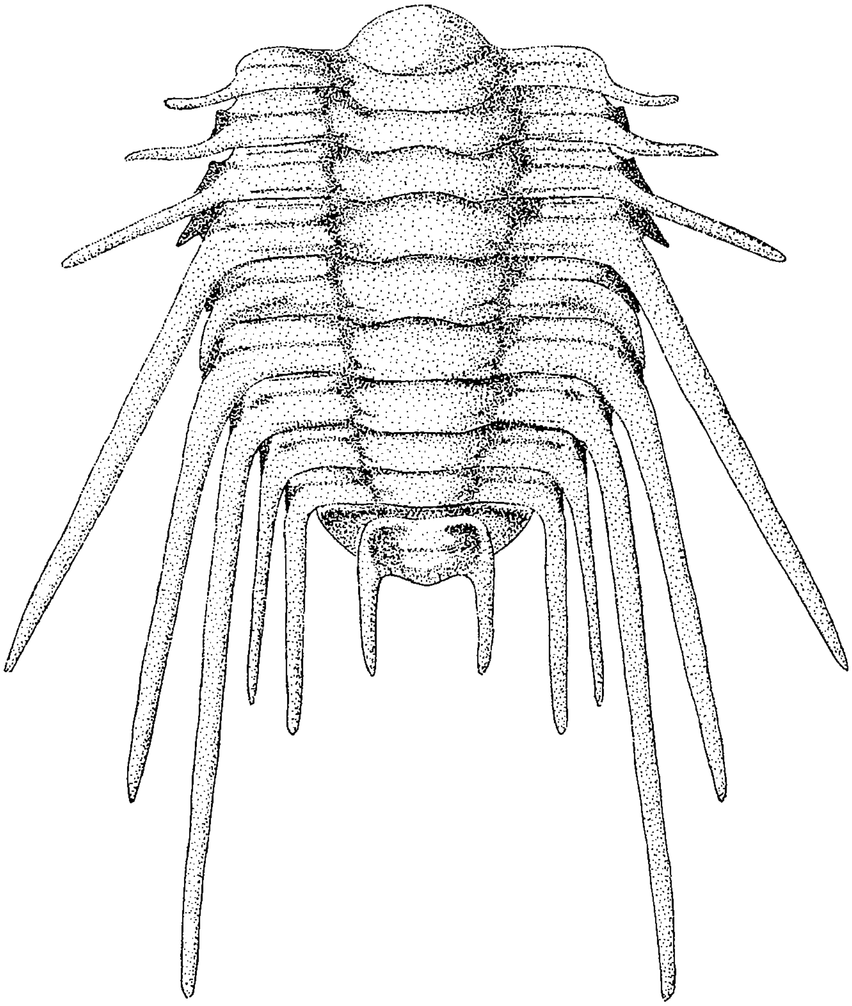
Free cheek has an expanded anterolateral border differentiated more by a break in slope than a border furrow; border apparently disappears beneath the genal spine, where there is a deep indentation in its outline; posterior border furrow is continuous on to the edge of the free cheek, demonstrating that the border in this region is subsumed into the base of the genal spine; surface of free cheek is steep and convex below the eye and is separated from the base of the genal spine by a very shallow furrow; eye is not well preserved but apparently was high and situated on a low pedicel.

Cephalic ornament consists of scattered tubercles on the cranidium and on the free cheeks in front of the eyes; a row of about 10 such tubercles is prominent along the eye ridge; another row lies between the eye ridge and the axial furrow, extending back adaxial of the base of the palpebral lobe, thus rendering the indistinct glabellar outline a little clearer than it would otherwise be; there are fine granules between these tubercles and over the remainder of the dorsal surface; granules are present in axial, occipital, and parts of the longitudinal furrows but sparse or absent in the glabellar furrows and other parts of the longitudinal furrows; granules are present on the occipital spines, and an enlarged tubercle lies on the ring just behind the occipital furrow; a single tubercle is developed on the posterior border behind the eye.

Doublure of free cheek is smooth, and it is narrowest at the rostral plate, broadening evenly to the anterolateral extremity and then diminishing to ω; a distinct antennular notch is present below α; rostral plate is not preserved in any specimen, but its form as determined from the surrounding structures is almost rodlike, with highly acute extremities, an almost straight posteroventral edge, and a slightly convex anterior edge.

Hypostome is transverse, length/width ratio is about 1/2; anterior edge is almost straight; middle body is flattened and is almost triangular in outline but has a slight depression (a remnant of the middle furrow) in the anterolateral corner; border furrow is shallow anteriorly but deepens and broadens abruptly into a posterolateral depression and then shallows medially; posterior and lateral borders mainly slope down into the border furrow, but in the position of the posterior wing they flexed outward into a prominence that breaks the even curve of the outline; posteriorly, the border narrows markedly to produce a wide, deep embayment in the outline; anterolateral corners are turned down into short, squat, anterior wings; lateral notch is about two-thirds the total hypostome length; doublure is uniformly broad laterally, but posteromedially it forms a tonguelike vertical extension, on the posterior face of which are 3 or 4 coarse terrace lines.

Thorax has axial rings that are highly and evenly arched on first 2 segments, tending to be a little flattened on the 3d, and then progressively developing a pair of low, rounded nodes on subsequent segments; in lateral profile, the 1st axial ring and, to a lesser extent, the 2d axial ring are directed posterodorsally, but subsequent rings are almost vertical from the pleurae; on all segments apodemal furrows are slitlike and directed posteromedially, and there is a shallow, vertical furrow rising from the edge of the posterior pleural band; these 2 furrows tend to isolate a convex lobe on the flank of each ring; this lobe is only partly separated from the principal pleural ridge by the shallow axial furrow; ring of first segment is short and merges into the articulatory furrow, which then rises abruptly onto the long articulatory half ring; the ring/articulatory half-ring length ratio is about 1/2; on subsequent segments the ring is better defined and proportionately longer, the above ratio becoming almost 1/1. Pleurae of all segments have a prominent, convex posterior pleural band and a less prominent anterior one; all segments, except possibly the last two, have pronounced anterior and posterior articulatory flanges. Posterior pleural spines on first 3 segments are short and more or less laterally directed; 4th spine is much enlarged, probably equal to the total axial length of the trilobite, and is posterolaterally directed; 5th spine is reduced, being a little shorter even than the 1st, and directed posterolaterally; 6th and 7th again are enlarged, but not as much as the 4th; 8th is greatly reduced, and the 9th is only a little larger; all spines subsequent to the 4th are progressively more posteriorly directed. Pleura is turned down to produce a squared terminus beneath the spine bases and be-



Text-figure 34. Reconstruction of thorax and pygidium of *Dicranurus hamatus elegantus,* new subspecies, from Haragan Formation. Note particularly shapes of anterior and posterior pleural spines.

tween this and leading edge of pleura there is a distinct articulatory notch; on the 1st segment this notch is greatly reduced; ventrolaterally directed anterior spine is developed from the squared terminus; anterior spines are absent from the 1st segment but well developed on the 2d and all subsequent segments, including the 5th; form of spine is "boot shaped," the toe of the boot being pointed posteriorly. Posterior pleural band of each segment has a distinct tubercle a short distance in from the fulcrum on the first segment, and a little farther adaxially on subsequent segments; crests of axial rings, posterior faces of articulating half rings, pleural furrows, the posterior flanges, and the anterior pleural spines, are all covered with granules; posterior pleural spines are apparently less densely granulose, at least on the dorsal surface; pleural ridges are apparently smooth.

Pygidium is subtriangular but has no terminal spine or projection; axis is two-thirds the pygidial length (excluding the articulating half ring) and has a bluntly rounded terminus; both axial rings have a pair of blunt nodes, the posterior pair being by far the smaller; pleural ridge is narrow, rounded, directed almost laterally, and then sharply bent posteriorly; a small node is present on the ridge at this angle; spines given off marginally are inclined upward a little from the plane of the pygidium; spines are somewhat longer than the axial pygidial length. Dorsal surface, and the whole surface of the marginal spines, are granulated. Doublure is narrowest at the anterolateral corners and increases regularly in size to the midline.

Remarks.—I have examined a large number of cranidia of *D. hamatus* (Hall) from the New Scotland Formation at Clarksville, New York, now in the collection of Yale University's Peabody Museum. These form the basis of the distinctions set out in the diagnosis of *D. hamatus elegantulus.* I have not been able to make direct comparisons of the thoraxes or pygidia.

The cranidium of *D. monstrosus* (Barrande) is probably closer to *D. hamatus* than to the Haragan subspecies. This is seen particularly in the diameter of the occipital spines and the coarseness of the tuberculation. Other distinctive features are displayed by the pygidium of *D. monstrosus.* This pygidium has a terminal protuberance, highly oblique pleural ridges, and paired spines that are given off from the border more dorsally than in *D. hamatus elegantus.*

The species *D. longispinus* (Mitchell), from the latest Ludlovian Rainbow Hill Marl Member (formerly Middle Trilobite Bed; see Link, 1970) at Yass, New South Wales, Australia, has a cranidial shape and ornament, occipital spines, and pygidial pleural ridge and axial terminus quite similar to those of *D. hamatus elegantus.* Its hypostome also is entirely comparable. The posterior pleural spines on the first three thoracic segments are probably longer, and the marginal pygidial spines are more convergent. *D. kinglakensis* Gill, from the Yeringian of Victoria, Australia (Gill, 1947), is also quite similar. Gill's comments that the occipital spines of these two species are not spirally recurved, and that the thorax and pygidium of *kinglakensis* are of altogether different construction, have not been substantiated.

Other material.—A few unnumbered specimens from the Haragan Formation at Old Hunton Townsite are in the OU collections. OU 5279 from the Haragan Formation at sec. 19, T. 2 S., R. 3 E., Murray County. One specimen from the Bois d'Arc Formation, 4 miles southeast of Wapanucka, SE¼NW¼ sec. 9, T. 3 S., R. 9 E., Atoka County, Amsden collecting locality A2-C.

Order LICHIDA Moore, 1959

Superfamily LICHACEA Hawle and Corda, 1847

Family LICHIDAE Hawle and Corda, 1847

Subfamily LICHINAE Hawle and Corda, 1847

Genus **Echinolichas** Gürich, 1901

Type species.—*Lichas eriopis* Hall, 1863, from the Onondaga Limestone (Middle Devonian) of New York.

Remarks.—The type species is poorly known and consists of dissociated material from several localities. One cannot be sure that the cephalons and pygidia have been correctly associated, and it is not clear that all the pygidia figured by Hall and Clarke (1888) are conspecific. The genus therefore, is virtually uninterpretable at present.

In his original designation of *Echinolichas,* Gürich (1901, p. 530) linked *L. bigsbyi* Hall with *L. eriopis.* Subsequently, Phleger (1936) and Tripp (1958) assigned *Lichas bigsbyi* to *Echinolichas,* though no reasons were given. The new Haragan species described herein has a similar cranidium, hypostome, and pygidial pleurae to those of *L. bigsbyi,* and in my opinion the species are clearly congeneric. They do seem to have some features in common with the cranidium of *L. eriopis* figured by Hall and Clarke (1888, pl. 19a, figs. 2-5), but they differ at least in the possession of a strong median basal lobe and definite though small occipital lobes. According to the definition given by Tripp (*in* Moore, 1959), these features alone would be enough to exclude the species from *Echinolichas.* The pygidia of the Haragan species differ from all those figured by Hall and Clarke in the shape of the pleural bands (particularly on the first segment), the pleural spines, and the tuberculation. Consequently, an assignment to *Echinolichas* can be regarded as tentative only, but it is deemed unwise to erect a new genus for the Haragan species until *E. eriopis* is revised.

Dimorphism.—Almost nothing is known of dimorphism in lichids. No study showing dimorphism at any one locality has yet been published. Warburg (1939) figured two types of *Hopolichas dissidens* (Beyrich) from loose boulder material of the Chiron or Lower *Chasmops* Limestones in the North Baltic, but these are placed in different "*varieties.*" It is interesting that one of the features in which these two types differ is the strength of the projection on the fronto-median lobe. The two types of *E*? *coccymelum* described below also differ in the degree of inflation of this lobe. The difficulty with interpreting these specimens as dimorphs is that they, like Warburg's specimens, cannot be shown to occur in the same stratum at the same locality. I have refrained from describing them as separate taxa, as more carefully collected specimens are required.

Echinolichas? bigsbyi (Hall)

Pl. 39, figs. 2, 6-8

Lichas bigsbyi HALL, 1861, p. 364, pl. 77, figs. 1-8.
Non *Lichas (Conolichas) bigsbyi* Hall; HALL and CLARKE, 1888, p. 80, pl. 19a, fig. 1.
Echinolichas bigsbyi (Hall); TRIPP *in* Moore, 1959, p. 498, fig. 392(2c).

Remarks.—There are several errors in the description and figures of this species given by Hall (1861). No subsequent description seems to have been given. The type material consists mainly of internal molds, and these may be very misleading. Attention is drawn to the following points:

1. The axial part of the basal lobe is quite well developed. It stands above the area in front, but the two regions are separated by a change in slope rather than by a distinct furrow. The ornament shows no break at the junction.
2. The lateral occipital lobes are clearly present, but they are small. They are transversely tear shaped and extend out behind the fixed cheek.
3. The ornament on the glabella is not as uniform as Hall indicates. Between the coarse tubercles there are finer ones, at least on the fronto-median lobe and on the tricomposite lobes. They may be more extensive than this.
4. The anterolateral corners of the hypostome are more angular than shown on plate 77, figure 7, by Hall. The maculae are better developed, and the middle furrow is not continuous medially on the better preserved of the two available specimens. The posterior furrow is close behind the maculae and is poorly defined. The ornament of the central body consists of flat tubercles. There are coarse terrace lines on the margin in the region of the anterior wings, and a few small scattered tubercles on the border below these. Elsewhere, the borders are smooth except in the vicinity of the posterior border furrow, where there are fine scattered pits.
5. The pleural tips on the pygidium are not well enough preserved to be certain of their shape, but they are certainly not as pointed as is shown on Hall's plate 77, figure 8, and the junctions between the pleural spines are not as acute.
6. The 2d pygidial pleural furrow and the 1st interpleural furrow are not as sinuous as Hall indicates.

In order to clarify these matters, the types are refigured herein.

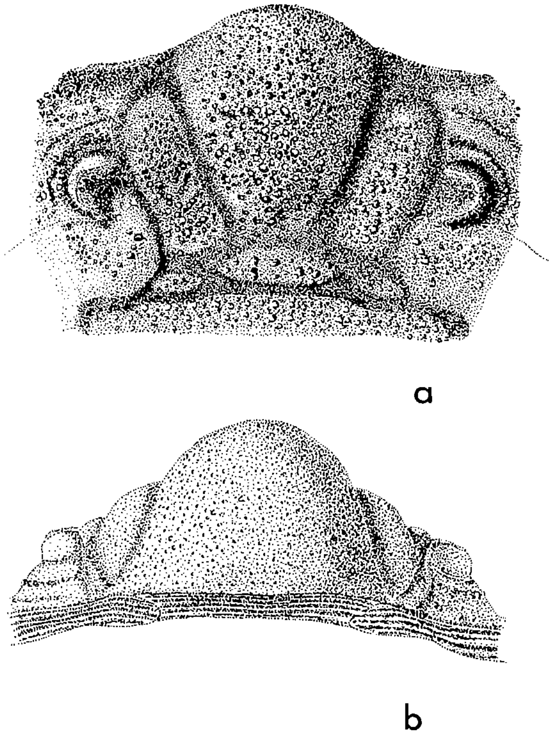
Echinolichas? coccymelum, new species

Pl. 38, figs. 1-3; pl. 39, figs. 1, 3-5;
pl. 40, figs. 2, 3

Types.—Holotype: OU 4962a-c, from the Haragan Formation, scree slope above bench at Old Hunton Townsite, NW¼, sec. 8, T. 1 S., R. 8 E., Coal County. Paratypes (Type A): OU 6533-5a-b and OU 6537, from the Haragan Formation, Old Hunton Townsite; and OU 6536 from the Haragan Formation along top of ridge to the north of the South Fork of Jackfork, sec. 4, T. 3 N., R. 6 E., Pontotoc County, near Amsden collecting locality P-1. Paratypes (Type B): OU 3446, from the Haragan Formation, outcrop at south end of exposure northeast of Bromide, Coal County; and OU 6538, from an unknown locality in the Haragan Formation.

Diagnosis.—A large species with cephalon up to approximately 4 cm long. Fronto-median lobe of glabella is high and either domed or produced into a cone; lateral glabellar lobes are tricomposite, with the basal one much narrower than the others; median basal lobe is well defined; lateral occipital lobes are present but weak; anterior border is short; cranidial ornament consists of moderately coarse tubercles and finer ones between them; pygidium has rounded to subrounded tips on the pleurae; anterior band of third pleura reaches the axial furrow.

Description of Type A.—Overall outline of cephalon is unknown, but probably has a length equal to half the width; cranidium extends well forward, forming a protrusion in the anterior outline of the cephalon. Glabella, in lateral profile, rises gradually from the occipital region in a gradually increasing angle to the very high crest a little forward of the midlength of the fronto-median lobe, then drops abruptly to the anterior border, which, in large specimens, it overhangs slightly; in anterior profile fronto-median lobe stands 1.5 to 2 times as high as the tricomposite lobes, both being well rounded. Occipital ring forms the widest part of the glabella, and in posterior profile almost conforms to the arc of a circle; ring is longest behind the longitudinal furrows, only slightly shorter medially, but tapers more markedly lateral to the occipital lobe; greatest length measures about 0.15 times the total glabellar length. Occipital lobe is quite small, almost imperceptible on large specimens but proportionately larger on small specimens. Basal glabellar lobe is clearly defined axially, is raised well above the surrounding areas, but laterally forms the attenuated posterior end of the tricomposite lobes. Median glabellar lobe is barely distinguished from the fronto-median lobe axially by a slight change in slope that swings forward into the axial furrows; on large specimens, the tricomposite lobes have a faint indentation just forward of the above junction and approximately on a line joining δ-δ of the facial suture; this indentation is most clearly seen on the smallest specimen, an internal mold (see Remarks). Axial furrow is broad and shallow throughout and is continuous around the entire glabella; furrow runs forward and inward until it is opposite the lateral basal glabellar lobe, then turns outward to beyond the palpebral area, finally forming a broad arc inward to join the anterior border furrow. Longitudinal furrow is similar in type to the axial furrow and is turned outward slightly at its anterior end to meet the axial and anterior border furrows together. Anterior border is very short, is formed of a sharp upturned lip laterally, and almost disappears medially.



Text-figure 35. Reconstruction of cranidium and inner parts of free cheeks of *Echinolichas? coccymelum,* new species, from Haragan Formation, shown in dorsal (*a*) and anterior (*b*) views.

Rostral suture lies just below the anterior margin; α-α is approximately equal to the distance between the crests of the lateral occipital lobes; β is about 2 mm from the axial furrow opposite the end of the longitudinal furrow and lies on a broad even arc; palpebral lobe is almost semicircular; ω is obscured, but posterior limb of suture runs directly laterally from ϵ at first and then arches obliquely backward; connective suture is strongly convex adaxially; hypostomal suture is slightly more arched than the rostral suture, producing a rostral plate that is shorter sag. than exsag.; hypostomal suture runs laterally from the rostral plate across the broad doublure, terminating almost directly below β. Only a small part of the doublure lateral to the rostral plate is known; this increases rapidly in length (exsag.) laterally; a deep, wide antennal furrow is present beneath the axial furrow; doublure and rostral plate are crossed by coarse, irregular terrace lines, spaced at 0.3-0.6 mm on the rostral plate and 0.5-1.1 mm on the doublure.

Palpebral lobe is small, only one-sixth the length of the glabella, and is flat on top, where it is ornamented with a few tubercles; palpebral furrow is deep and wide, separating the palpebral lobe from the moderately inflated fixed cheek between it and the axial furrow. Free cheek is poorly known; border apparently is concave overall but has a sharp crest along the margin; border furrow is poorly defined. Visual surface of eye covers almost a semicircle in plan and is strongly convex in anterior profile, being highest near its anterior extremity and gradually and evenly diminishing in height posteriorly; visual surface surmounts a narrow vertical band, is set on a broad parapetlike socle, and fades away abruptly in front of the facial suture.

Cranidium has two orders of tubercles showing a distinctive distribution pattern; first-order tubercles are largest (up to 1.3 mm in diameter) on axial parts of basal and median lobes, diminishing progressively to the anterior border; shape shows a corresponding topographical change from circular or ovate symmetrical mounds to more arcuate ones with a gentle anterior and an abrupt posterior face; secondary tubercles (0.1-0.2 mm in diameter) show a similar distribution of shape types, but tend to be more closely spaced anteriorly. On tricomposite lobes also, tubercles decrease in size anteriorly, but never reach the size of the largest ones on the axial region. Largest tubercles of all are on free cheeks anterior and lateral to the eye platform and continue down into anterior border furrow; slightly smaller tubercles are present on fixed cheek behind palpebral lobe; on fixed cheek posterolateral to eye, only small tubercles (0.1-0.3 mm in diameter) are present.

Hypostome has a low profile, width is a little greater than length; ignoring the posterior notch, outline is almost circular; middle body is pear shaped in outline, reaching the hypostomal suture, and is defined laterally by broad shallow furrows that become narrower and sharper both anteriorly and posteriorly from about the midlength of the middle body; middle furrow is quite faint; maculae are prominent, sharply defined, ovate, with their long axes at 45° to the axial line; lateral border is broad and forms a prominent "cat's ear lobe" in the sense of Tripp (1957); a distinct broad depression is present on the anterior two-thirds of this lobe, and within this are two smaller depressions, one lateral to the macula and the other a short distance behind that; posterior notch is about one-sixth the length of the hypostome, on some specimens tending to be U-shaped in outline; posterior extremities are well rounded; central body and anterior two-thirds of cat's ear lobes are ornamented with fine pits and tiny, flattened, scalelike ridges, each rising gently at the front and vertical at the back; region on border posterior to the anterior wings has terrace lines that extend onto the wing; surface posterior to central body is smooth; anterior wings are vertical; anterior margin is upturned to form a vertical wall along the hypostomal suture; there is a pronounced lateral notch behind the anterior wing, forming only a slight notch in the ventral outline; doublure is wide posteriorly and forms a vertical wall at the anterior end of the notch.

Pygidium is transverse, width is probably twice the length; axis is poorly known, but high, and probably was either unsegmented or poorly segmented; posterior end of axis drops rather sharply, possibly from a large posterior node, and then flattens out into the posterior median pleural area; axial furrow is weak, slightly sinuous laterally, and incomplete posteriorly; fulcra are situated well out from the axial furrow, producing a long, straight anterior edge; pleural and interpleural furrows are of approximately equal depth and width and are well rounded to slightly angular at the base; 1st pleura expands abruptly in length (sag.) laterally, with its pleural furrow deriving from its anteromedial corner and oriented so as to produce anterior and posterior pleural bands of comparable length abaxially; 2d pleura is a little shorter (exsag.) than the first, with its pleural furrow meeting the first interpleural furrow a short distance out from the axial furrow, and with the anterior band remaining shorter (exsag.) than the posterior band, except distally; 3d pleura is poorly known but with pleural furrow meeting the axial furrow independently and dividing the pleura into approximately equal parts, proximally at least; 3d interpleural furrow is deflected forward into the axial furrow; median pleura is almost unknown. The one pleural tip preserved (pl. 40, figs. 3a, b), probably the second, is broadly rounded in outline. Ornament on pleurae consists mainly of tubercles graded in size from about 1.75 mm to 0.20 mm base diameter; largest tubercles form an irregular row along the middle of each anterior and posterior band; tubercles are well preserved and have an apical perforation; similar tubercles are present on axis, but their distribution is unknown; distally, pleurae have increasing numbers of scalelike prominences and decreasing numbers of tubercles; scalelike structures are arcuate in outline, lie subparallel with the pygidial margins, and have gentle adaxial and steep abaxial faces. Doublure is about half the width of the pleurae and is crossed by very coarse terrace lines and a mat of very fine granules.

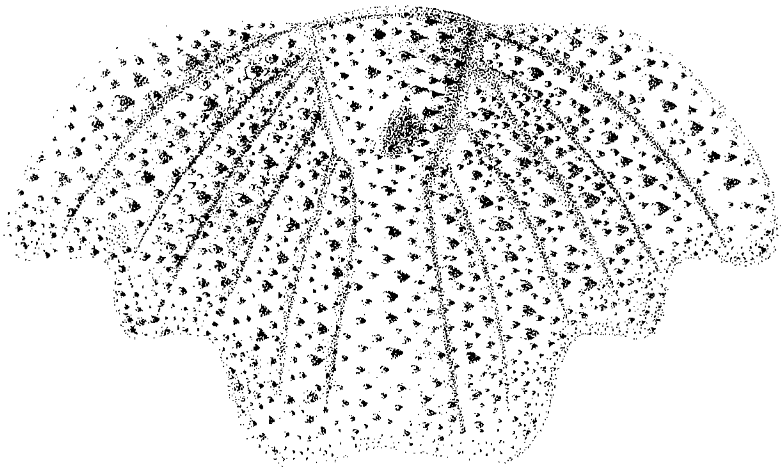
Remarks.—The material of this morph of the species is incomplete, the genal regions, the thorax, and the margins of the pygidium being unknown. The most complete cranidium, OU 6534, is the internal mold of a juvenile holaspid. This is a particularly important specimen because it shows most clearly the subdivisions of the tricomposite lobes (pl.' 39, fig. 1). Whittington (1963, p. 104-105) commented on the extent of the difference in strength of the various furrows of the dorsal exoskeleton in lichids, particularly in cases where the skeletal material has been partly or completely exfoliated.

This new species can be distinguished readily from *E*? *bigsbyi.* In *E*? *coccymelum,* (a) the tricomposite lobes are relatively wider (tr.) and flatter; this implies that the longitudinal and axial furrows are shallower; (b) the occipital lobes are smaller and less distinct; (c) the axial part of the basal lobe is more prominent; (d) the anterior border of the cephalon is less prominent; (e) the hypostome is less angular anterolaterally, the furrow in the cat's ear lobe is only vaguely connected to the lateral furrow, and the ornaments of both the central body and the lateral borders are distinctive; (f) the pygidium is wider between the fulcral points, and there is less curvature along the anterolateral margins; (g) the anterior bands on all three pygidial pleurae are larger; also, associated with this, the anterior band of the third pleura reaches to the axial furrow; (h) the marginal pygidial spines are much more rounded.

Other material.—There are a few unnumbered fragmentary specimens from Old Hunton Townsite.

Description of Type B.—One almost complete cranidium and one small fragment of a fronto-median lobe are referred to this taxon. There is a basic similarity to Type A in the plan of the various cranidial lobes and furrows, but there are also several striking differences:

1. The fronto-median lobe is much higher and conical in shape. In lateral profile its



Text-figure 36. Reconstruction of pygidium of *Echinolichas*? *coccymelum,* new species, from several specimens from Haragan Formation, supplemented, in part, by Hall's material of *E.*? *Bigsbyi* (Hall) from New Scotland Formation. Margins, particularly at posterior extremity, involve some inference, for they have not been found complete in any specimen.

anterior face is almost vertical, and its posterior face is inclined at about 60° to the horizontal.

2. The tricomposite lobes are proportionately a little shorter.

3. The median part of the posterior glabellar lobe is slightly pronounced.

4. The various furrows on the cranidium are wider and more pronounced.

5. The tuberculation is coarser and higher, particularly on the fronto-median lobe, and there are few secondary tubercles between the primaries, except on the anterior of the fronto-median lobe, where they are quite small. Tubercles are sparse on the posterior of the fronto-median lobe, but they are crowded toward its apex. The largest tubercles have a diameter of 1.3 mm at their bases.

6. The occipital lobe is so reduced as to be represented by a single tubercle.

Remarks.—No pygidia have been found associated with the two cranidia. It is possible, however, that some of the pygidia described above under Type A belong to this form.

Genus **Terataspis** Hall, 1863

Type species.—*Lichas grandis* Hall from the Lower Devonian of New York.

Terataspis? sp.

Pl. 40, fig. 1

Description.—One fragment of a cranidium is all that is available. Occipital ring has at least five large, rounded, slightly posteriorly inclined tubercles near its posterior edge and numerous smaller tubercles scattered irregularly in front; there is also a row of smaller tubercles along the posterior margin of the ring below the large tubercles; occipital furrow is shallow and also contains a few tubercles; other parts of occiput were not observed. Median basal lobe is slightly raised and is covered with tubercles like those on the front of the occipital ring; posterior parts of lateral glabellar lobes bear 1 or 2 large tubercles like those on the rear of the occipital ring, but the surface is raised only slightly above the level of the axial region.

Remarks.—This fragment has essentially the same occipital structure and tuberculation as *T. grandis,* but the basal parts of the lateral glabellar lobes are much flatter than those of that species. Moreover, the tuberculation of these lobes is relatively subdued. This could be due to the disparity in size of the forms compared, the Oklahoma individual being only one-third the size of those figured by Hall and Clarke (1888, pls. 17, 18).

Material.—OU 7192 from the Frisco Formation, SW¼SW¼ sec. 13, T. 13 N., R. 23 E. (S1-B), Sequoyah County.

REGISTER OF LOCALITIES

(Section and interval designations, unless otherwise stated, are those of Amsden, 1960)

Haragan Formation

1. Old Hunton Townsite: NW¼ sec. 8, T. 1 S., R. 8 E., Coal County.

Undifferentiated levels
Cordania falcata
P. (Paciphacops) raymondi
Reedops deckeri
H. (Huntonia) purduei purduei
H. (Huntonia) lingulifer
H. (Huntonia) oklahomae
H. (Huntonia) huntonensis
H. (Huntonia), new form
Leonaspis williamsi
Dicranurus hamatus elegantus
Ceratonurus sp.
Echinolichas coccymelum

Near top of section
Otarion axitiosum
P. (Paciphacops) raymondi
Dicranurus hamatus elegantus
Echinolichas coccymelum

Section C1—H to J
Cordania falcata
P. (Paciphacops) raymondi
H. (Huntonia) oklahomae
H. (Huntonia) huntonensis
H. (Huntonia), new form

Section C1—K
Cordania falcata
H. (Huntonia) purduei purduei
H. (Huntonia) huntonensis
H. (Huntonia), new form
Dicranurus hamatus elegantus

Section C1—M to 0
Cordania falcata
H. (Huntonia) huntonensis
H. (Huntonia) oklahomae

2. Northeast of Bromide: SW¼NW¼ sec. 33, T. 1 S., R. 8 E., Coal County.

Undifferentiated levels
Reedops deckeri
H. (Huntonia) lingulifer
Echinolichas coccymelum

Section C2—G
P. (Paciphacops) raymondi
H. (Huntonia) lingulifer
H. (Huntonia) oklahomae

Section C2—H to J
P. (Paciphacops) raymondi
H. (Huntonia) purduei purduei
H. (Huntonia) lingulifer
H. (Huntonia), new form

3. Henryhouse Creek: SE¼ sec. 30, T. 2 S., R. 1 E., Carter County.
Section Ca1 (1)—W
P. (Paciphacops) raymondi

4. West of Tulip Creek: NW¼SE¼ sec. 25, T. 2 S., R. 1 E., Carter County.
Section Ca2—P
P. (Paciphacops) raymondi

5. West of Mill Creek: SE¼NW¼ sec. 12, T. 2 S., R. 4 E., Johnston County.
Section J11—D
P. (Paciphacops) raymondi
H. (Huntonia) purduei purduei

6. Vines dome: NW¼NW¼ sec. 2, T. 2 S., R. 2 E., Murray County.
Undifferentiated zones
P. (Paciphacops) raymondi
Reedops deckeri
H. (Huntonia) purduei purduei
Section M1—I
P. (Paciphacops) raymondi
Section M1—J
P. (Paciphacops) raymondi
Reedops deckeri
Section M1—K
P. (Paciphacops) raymondi
H. (Huntonia), new form
Section M1—L
Cordania falcata

7. White Mound: secs. 17 and 20, T. 2 S., R. 3 E., Murray County.
Undifferentiated levels
Dechenellid, new genus and species
Otarion axitiosum
Cordania falcata
P. (Paciphacops) raymondi
Reedops deckeri
H. (Huntonia) oklahomae
H. Huntonia huntonensis
Ceratonurus sp.
Dicranurus hamatus elegantus
Leonaspis williamsi
Section M2—M
P. (Paciphacops) raymondi
H. (Huntonia) huntonensis
Section M4
Otarion axitiosum
P. (Paciphacops) raymondi
Reedops deckeri
H. (Huntonia) oklahomae
H. (Huntonia), new form
Leonaspis williamsi

8. Southern Rock Asphalt Quarry: NW¼SE¼ sec. 25, T. 1 S., R. 2 E., Murray County.
Section M9—B
P. (Paciphacops) raymondi

9. Buckhorn Ranch: SW¼SE¼ sec. 33, T. 1 S., R. 3 E., Murray County.
Section M10—J
P. (Paciphacops) raymondi
Reedops deckeri
Section M10—M
P. (Paciphacops) raymondi

10. West of Highway 77: NW¼ sec. 30, T. 1 S., R. 2 E., Murray County.
Section M17—J
H. (Huntonia) oklahomae

11. Ridge north of south fork of Jackfork Creek: SW¼ sec. 4, T. 2 N., R. 6 E., Pontotoc County.
Near Section P1
Echinolichas coccymelum

12. North of Coal Creek: NW¼ sec. 22, T. 1 N., R. 7 E., Pontotoc County.
Section P9—J to K
P. (Paciphacops) raymondi

Bois d'Arc Formation—Cravatt Member

1. Four miles southeast of Wapanucka: SE¼NW¼ sec. 9, T. 3 S., R. 9 E., Atoka County.
Section A2—C
P. (Paciphacops) raymondi
Dicranurus hamatus elegantus

2. Old Hunton Townsite: NW¼ sec. 8, T. 1 S., R. 8 E., Coal County.
Section C1—P
Odontochile syncrama
P. (Paciphacops) cf. *P. birdsongensis*

3. Henryhouse Creek: SE¼ sec. 30, T. 2 S., R. 1 E., Carter County.
Section Ca1—X
P. (Paciphacops) cf. *P. birdsongensis*
Section Ca1(2)—S2
P. (Paciphacops) cf. *P. birdsongensis*

4. South of Sulphur: quarry near Highway 18, SW¼ sec. 36, T. 1 S., R. 3 E., Murray County.
H. (Huntonia) lingulifer
H. (Huntonia) purduei purduei

5. South of Sulphur: quarry near Highway 18, SW¼ sec. 1, T. 2 S., R. 3 E., Murray County.
P. (Paciphacops) cf. *P. raymondi*
H. (Huntonia) lingulifer

6. South of Sulphur: SW¼SE¼ sec. 30, T. 1 S., R. 4 E., Murray County.
Section M11—E
P. Paciphacops cf. *P. birdsongensis*

7. Coal Creek: NW¼NW¼ sec. 22, T. 1 N., R. 7 E., Pontotoc County.
Section P9—0
H. (Huntonia) huntonensis

8. Quarry on north side of Highway 61, SW¼SE¼ sec. 1, T. 1 N., R. 6 E., Pontotoc County.
Section P13
H. (Huntonia) purduei purduei
Odontochile syncrama

9. Goose Creek: NW¼SE¼ sec. 26, T. 1 N., R. 6 E., Pontotoc County.
   Section P17—D
   Cheirurus sp.

Bois d'Arc Formation—Fittstown Member

1. Old Hunton Townsite: NW¼ sec. 8, T. 1 S., R. 8 E., Coal County.
   Section C1—Q
   H. (Prosocephalus) xylabion

2. Henryhouse Creek: SE¼ sec. 30, T. 2 S., R. 1 E., Carter County.
   Section Cal (2)—V(2)
   H. (Prosocephalus) xylabion

3. West of Mill Creek: SE¼NW¼ sec. 12, T. 2 S., R. 4 E., Johnston County.
   Section J11—L
   H. (Prosocephalus) xylabion

4. Buckhorn Ranch: SW¼SE¼ sec. 33, T. 1 S., R. 3 E., Murray County.
   Section M10—P
   P. (Paciphacops) invius

5. Cedar Hill: SE¼ sec. 4, T. 2 N., R. 6 E., Pontotoc County.
   Section P3—CC
   Breviscutellum sp.
   Section P3—GG
   P. (Paciphacops) invius
   Coniproetus sp.
   Section P3—JJ
   P. (Paciphacops) invius

6. Bois d'Arc Creek: sec. 11, T. 2 N., R. 6 E., Pontotoc County.
   Section P8—F
   Cheirurid undet.
   Section P11—A
   H. (Prosocephalus) xylabion
   Position unknown
   Phalangocephalus rutabulum

7. Collection P16: NE¼SW¼ sec. 35, T. 2 N., R. 6 E., Pontotoc County.
   Otarion cf. *O. axitiosum*
   P. (Paciphacops) cf. *P. birdsongensis*
   H. (Huntonia) purduei fittstownensis
   Odontochile syncrama

Frisco Formation

1. Canyon Creek Ranch: NE¼SE¼ sec. 7, T. 1 N., R. 7 E., Pontotoc County.
   5 feet above base of Ventress' section 3
   P. (Paciphacops), new species
   Dalmanitacean undet.

2. North of Coal Creek: NW¼ sec. 22, T. 1 N., R. 7 E., Pontotoc County.
   Section P9—R
   P. (Paciphacops), new species
   P. (Viaphacops), new species
   Base of Ventress' section 1
   P. (Viaphacops) cf. *P. (Viaphacops) bombifrons*

3. Southwest of St. Clair Lime Quarry: NW¼SE¼ sec. 14, T. 13 N., R. 23 E., Sequoyah County.
   Otarion sp.
   Odontochile ceraunus
   Dalmanitacean undet.
   Lichid undet.

4. Northwest of Sallisaw Creek: SW¼SW¼ sec. 13, T. 13 N., R. 23 E., Sequoyah County.
   Section S1—B
   Terataspis sp.

5. Payne Hollow: sec. 22, T. 13 N., R. 23 E.
   Section S8—C
   ?*Proetus* sp.

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PLATES

Plate 1

Figure 1. *Acernaspis elliptifrons* (Esmark). Anterodorsal view of cephalon with most of exoskeleton removed to show muscle insertions into anterior lobe. Palaeontological Museum, Oslo, 41745A, ×6.25. Llandoverian, Oslo.

Figures 2, 5. *Eophacops musheni* (Salter). Anterodorsal and lateral views of cephalon photographed under glycerine. Sedgwick Museum, A28671, ×5. Wenlockian, Dudley, England.

Figures 3a, b. ?*Cheirurus* sp. Dorsal and anterodorsal views. OU 6549, ×2. Cravatt Member, locality P17.

Figures 4a, b. Cheirurinid, genus and species undet. Ventral and lateral views of hypostome. OU 7191, ×2. Fittstown Member, locality P8—F.

Figures 6a, b. Calymenid, genus and species undet. Posterodorsal and posterior views. OU 8259, ×4.5. Fittstown Member, locality P3—JJ.

Figure 7. *Breviscutellum,* new spcies. OU 6548, ×3.5. Fittstown Member, locality P3—CC.

Figure 8. Scutelluid, genus and species undet. OU 6820, ×3.6. Haragan Formation, locality M4.


4b

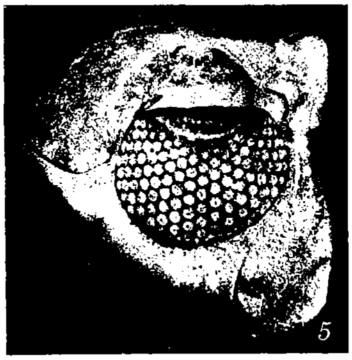

4a


1


2


3a


3b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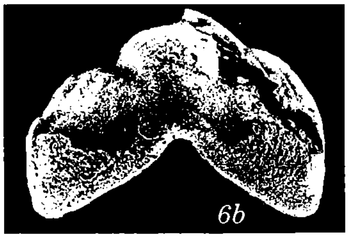
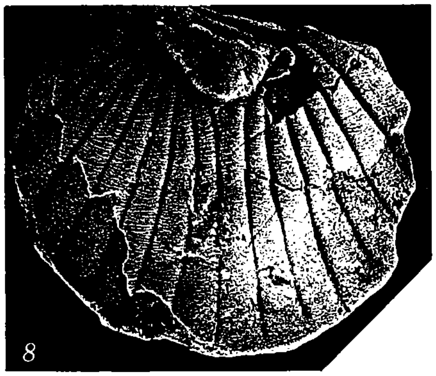
6a


6b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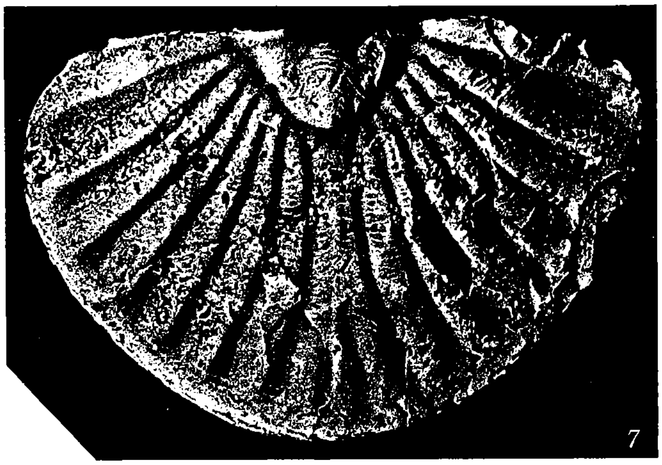
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Plate 2

Figures 1a, b. ?*Proetus*, species undet. Dorsal and oblique posterior views. OU 8262, ×1.25 and ×2. Frisco Formation, locality S8—C.

Figures 2-9. *Otarion* sp. A., all from Frisco Formation, southwest of St. Clair Lime Quarry, Sequoyah County.

Figure 2. Latex cast. OU 6594E, ×5.

Figure 3. Internal mold. OU 6594W,. ×4.

Figure 4. Partial internal mold. OU 6594, ×4.

Figure 5. Internal mold. OU 6594P, ×8.

Figures 6, 9. Two views of internal mold. OU 6594P, ×5.

Figure 7. Internal mold of cranidium and interior of part of cheek. OU 6594A, ×4.7.

Figure 8. Latex cast. Note palpebral lobes. OU 6954Y, ×6.

Figures 10a, b. *Coniproetus* sp. Dorsal and oblique views of cranidium. OU 6550, ×4.6. Fittstown Member, locality P3—GG.

Figures 11a, b. *Coniproetus* sp. Dorsal and oblique views of pygidium. OU 6551. ×6. Same locality.

Plate 2

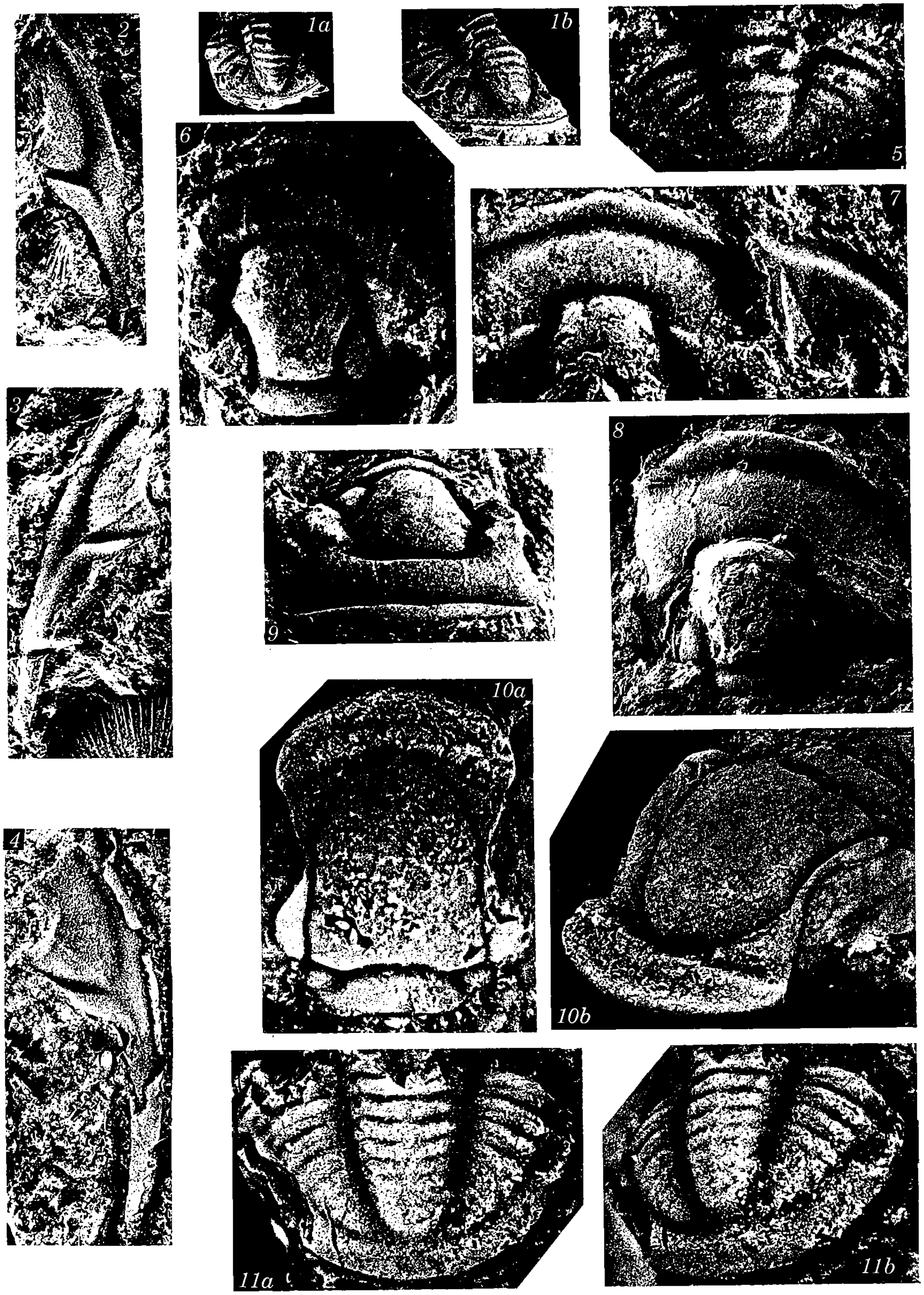


Plate 3

Figure 1. *Otarion* cf. *O. axitiosum.* Two specimens, right one with anterior border destroyed. OU 7196E, ×15. Fittstown Member, locality P16.

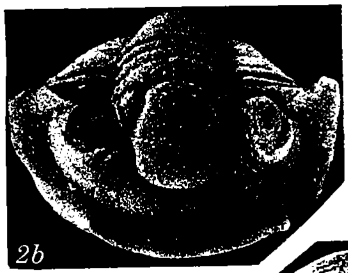
All other figures *Otarion axitiosum,* new species; all specimens are from Haragan Formation.

Figures 2a-c. Dorsal, anterior, and ventral views of average-sized specimen. USNM 139170, ×7.5, ×8.5, and ×8.0. Near Nebo, Murray County.
Figures 3a, b. Dorsal and anterior views of well-preserved specimen. OU 6552A, ×7.5 and ×8.6. Sec. 19, T. 2 S., R. 3 E.
Figure 4. Dorsal view. OU 6552B, ×10. Same locality.
Figures 5a, b. *a,* Dorsal view of large specimen with details of thoracic ornament and almost complete genal spine. Anterior border displaced forward. *b,* posterodorsal view of pygidium and last two thoracic segments. OU 6554, ×10 and ×19 approx. Locality C1.
Figure 6. Two incomplete specimens showing scattered tubercles on cephala. Anterior border on right specimen is cut away to show rostral plate. OU 5284, ×13. White Mound.


5b


1


3b

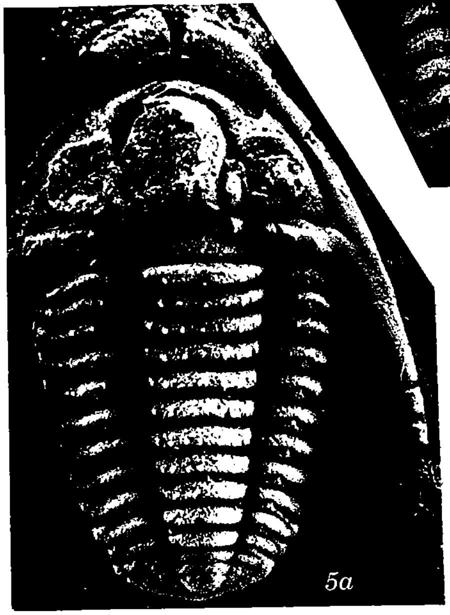

2b


2a


2c


3a


4


5a

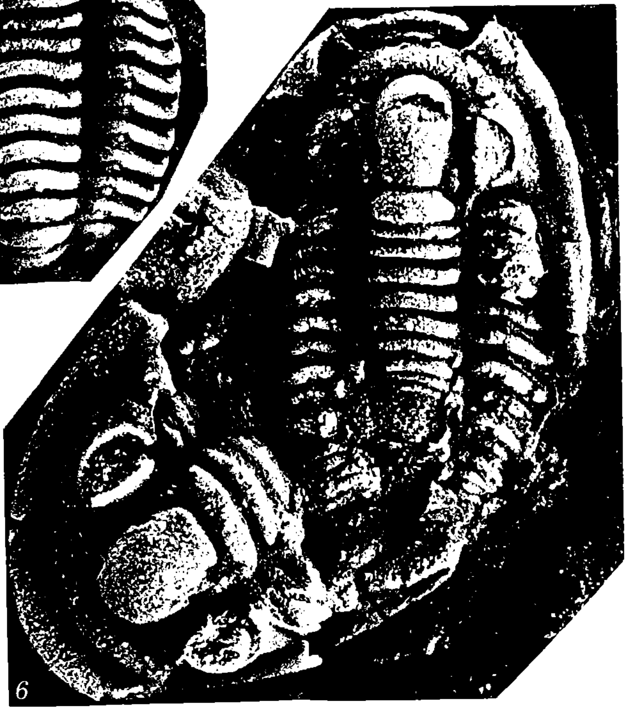

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Plate 4

Figures 1, 2. *Cordania falcata* Whittington. *1,* almost complete specimen, and *2,* specimen with most of exoskeleton removed; note very fine terrace lines on inner part of doublure indicated by arrow. OU 5245, ×3.5, and OU 7193, ×3. Haragan Formation, Old Hunton Townsite and White Mound, respectively.

Figures 3, 4. *Huntonia (Huntonia) purduei purduei* (Dunbar). *3a,* latex cast of inner surface of axis of pygidium showing three pairs of apodemes, with cavities for muscle attachment indicated by arrows. *3b,* right side of same specimen; USNM 143113D, ×3. *4,* latex cast of inner surface of glabella showing shapes of occipital and 1p apodemes. USNM 143113B, ×2. On both these specimens, latex has not penetrated to deepest parts of molds.

Figure 5. *Odontochile ceraunus,* new species. Latex cast of part of free cheek showing rounded anterior outline, border furrow, and second furrow adaxial to this. OU 8268, ×1.5. Frisco Formation, southwest of St. Clair Lime Quarry.

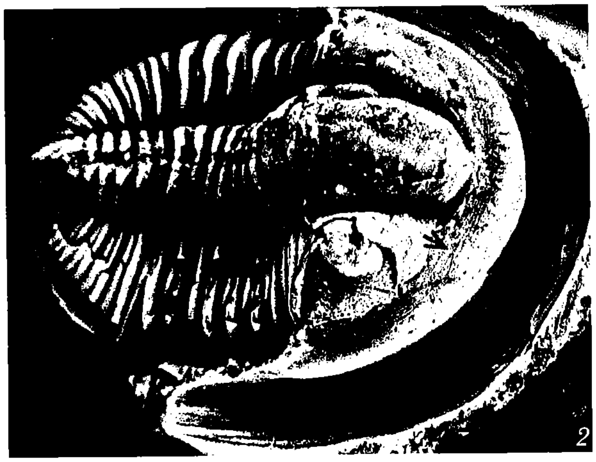
Figures 6, 8. *Odontochile ceraunus,* new species. Two isolated glabellae with most of exoskeleton removed. Note muscle insertion areas into anterior lobe. OU 8264A, ×1.5, and OU 8265, ×1.5. Same locality.

Figure 7. *Odontochile ceraunus,* new species. Internal mold of pygidium, with doublure showing on left. OU 8267, ×2. Same locality.

Figures 9a-c. Dechenellid, genus and species undet. Posterior, lateral, and dorsal views of pygidium retaining exoskeleton on right side. OU 6587, ×6. Haragan Formation, White Mound.

Plate 4


1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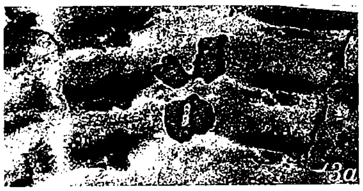
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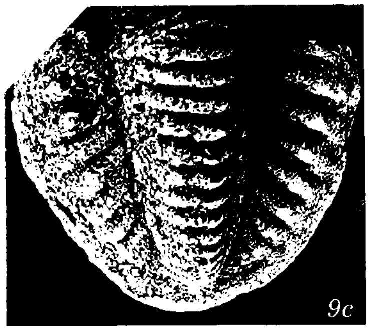
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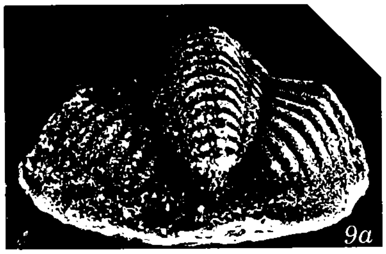
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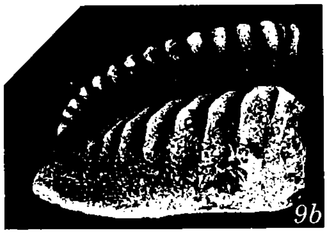
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Plate 5

All specimens *Cordania falcata* Whittington, from Haragan Formation.

Figure 1. Latex cast of cephalon viewed ventrally to show remarkable rolled doublure and connective suture (inked on left side). OU 7193, ×2. See also plate 4, Figure 2, for specimen from which cast has been made.

Figures 2a-d. Lateral, anterodorsal, anterior, and posterior views of almost complete specimen. OU 5243; *a*, ×5.3; *b-d*, ×3.5 approx. Old Hunton Townsite.

Figures 3a-c. Lateral, dorsal, and oblique views of specimen with genal spines removed. Note positions and shapes of pleural tips of thorax, and pygidial doublure. OU 5246, ×3.5. Old Hunton Townsite.

Figure 4. Anterior view of cephalon of second morph to show absence of wide border roll. ANU 14849, ×3.2. Clarita, Coal County (probably Old Hunton Townsite).


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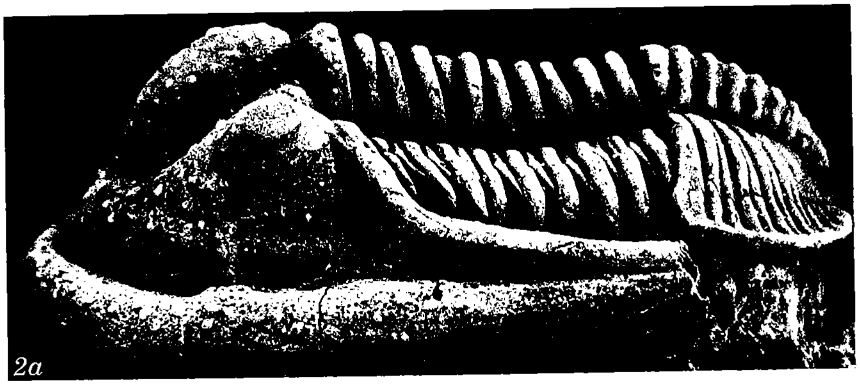
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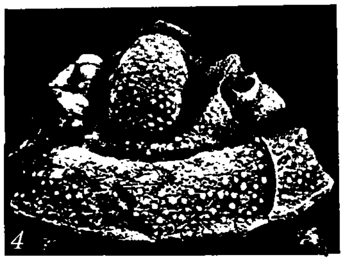
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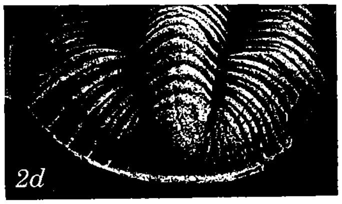
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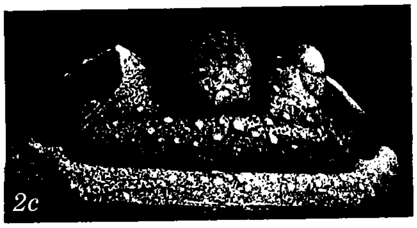
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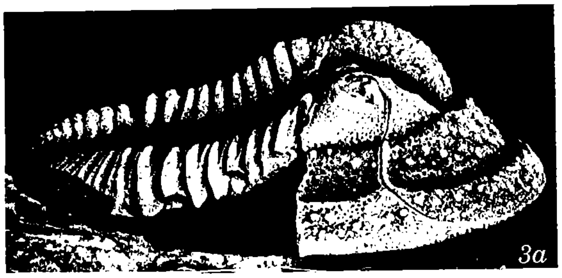
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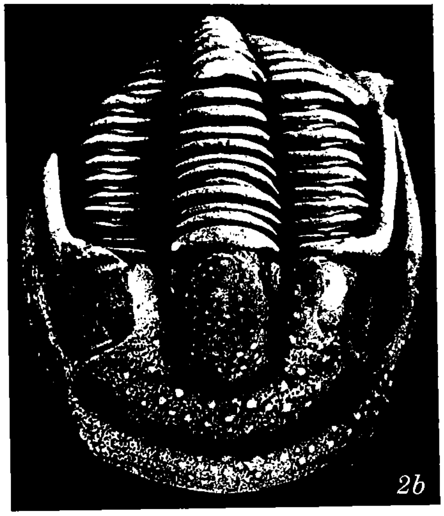
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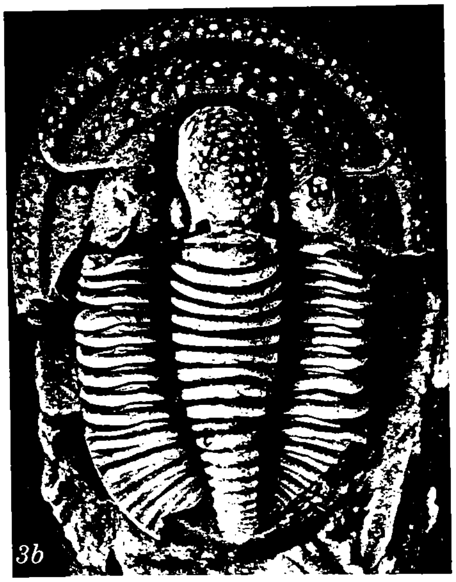
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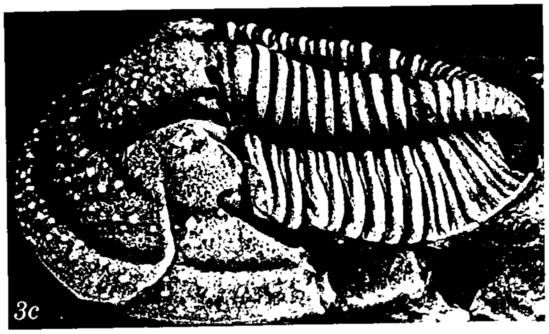
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Plate 6

Figure 1. *Paciphacops (Paciphacops) birdsongensis* (Delo). Part of anterior wall of glabella and border, showing large tubercles (*1*), granules (*2*), and fine perforations between tubercles (*3*). ANU 30591, ×20 approx. Birdsong Shale, Big Sandy River, Tennessee.

Figure 2. *Paciphacops (Paciphacops) birdsongensis* (Delo). Scanning-electron micrograph of small part of inner surface of front part of glabella and anterior-border glabella, showing collared internal apertures of perforations through granules. ANU 30592, ×80. Birdsong Shale, Big Sandy River, Tennessee.

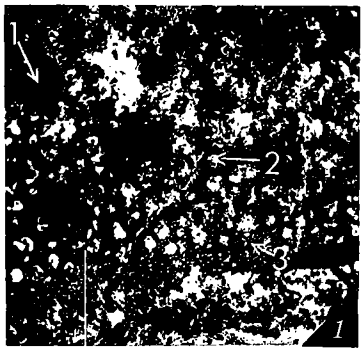
Figure 3. *Reedops deckeri* Delo. Partly corroded lenses, photographed under glycerine. OU 5377, ×19. Haragan Formation, Old Hunton Townsite.

Figure 4. *Paciphacops (Paciphacops) raymondi* (Delo). Specimen of large-eyed morph with lenses slightly corroded, and central core and annulus outlined by ferruginous staining. OU 6809, ×19. Haragan Formation, Old Hunton Townsite.

Figure 5. *Paciphacops (Paciphacops) raymondi* (Delo). Eye of small-eyed morph, partly removed by corrosion. Note beaded surface of sclera, dark line around each lens representing scleral membrane, and in center of several lenses (particularly one indicated by arrow) base of central core. OU 6814, ×19. Haragan Formation, Old Hunton Townsite.

Figures 6, 7. *Paciphacops (Paciphacops) birdsongensis* (Delo). Two specimens preserved as internal molds but with lenses partly replaced by silica. USNM 308982C and USNM 208982A, ×2.5 and 2.3. Ross Limestone, Pickwick Dam, Tennessee.

Figures 8-11. *Paciphacops (Paciphacops) birdsongensis* (Delo). *11,* specimen with most completely preserved lenses; symbols as in text; USNM 208982A, ×19. *9,* specimen with most of lenses completely removed from their cups (*C*); USNM 208981B, ×19. *8, 10,* two specimens with lens partly preserved, showing central cores and roughened contacts between intralensar bowl and upper unit; symbols as in text; USNM 208981A, ×23, and UNSM 208982C, ×25. All specimens from Ross Limestone, Pickwick Dam, Tennessee.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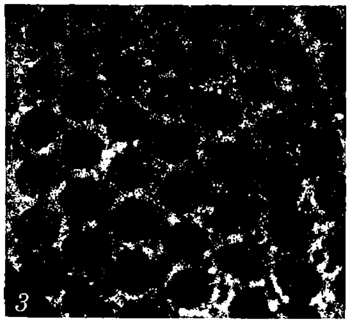
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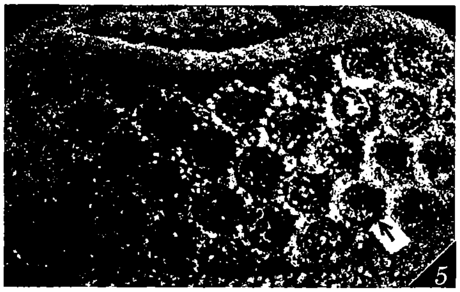
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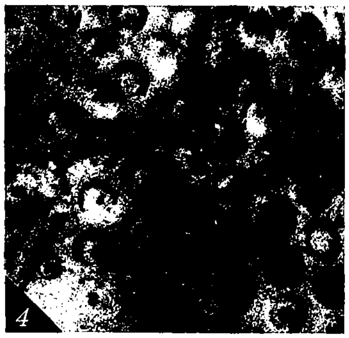
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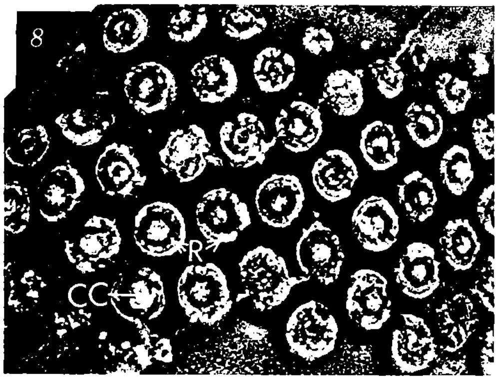
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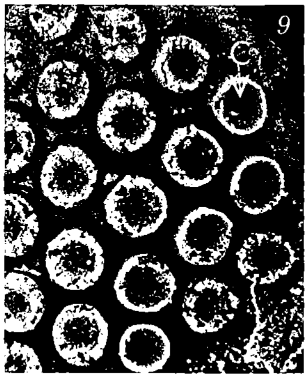
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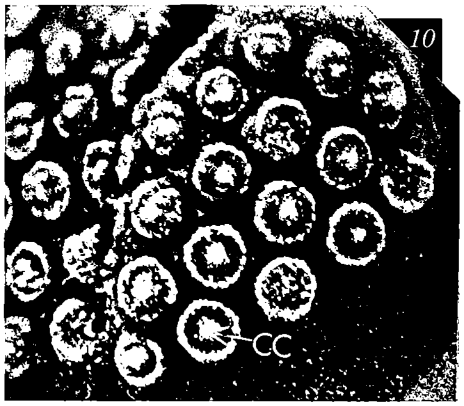
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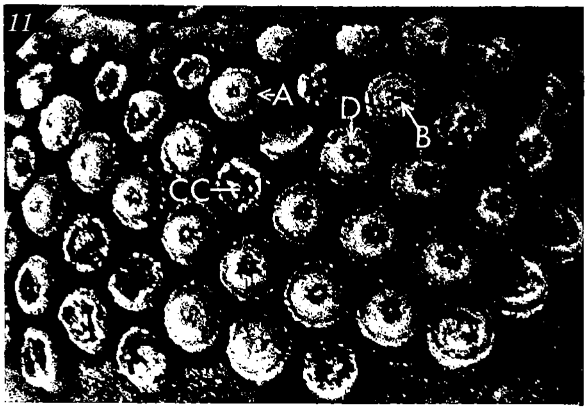
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A
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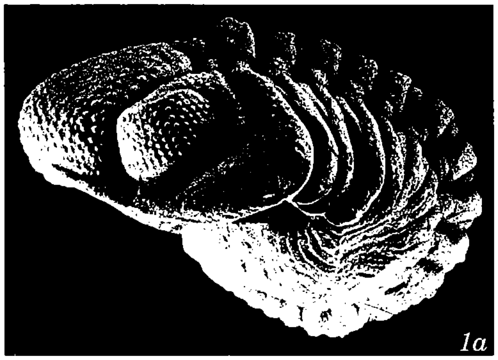
Plate 7

All specimens of *Paciphacops (Paciphacops) raymondi* (Delo), from Haragan Formation.

Figures 1a-c. Three views of almost complete specimen. OU 6810; *a, b,* ×3.5; *c,* ×4.0. Old Hunton Townsite.

Figures 2a, b. Cephalon with particularly well-preserved ornament. Note perforations in major tubercles. OU 8273, ×4.7 and ×12.5. Old Hunton Townsite.

Figure 3. Almost complete specimen. Compare weak pits for thoracic pleural tips in vincular furrow with their almost complete absence in figure 1c. OU 6809, ×3.2. White Mound.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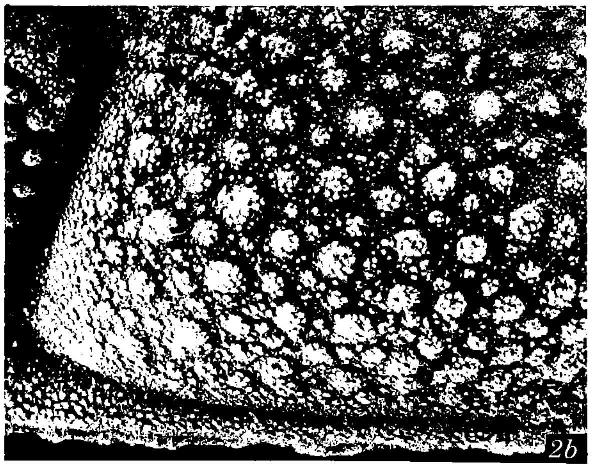
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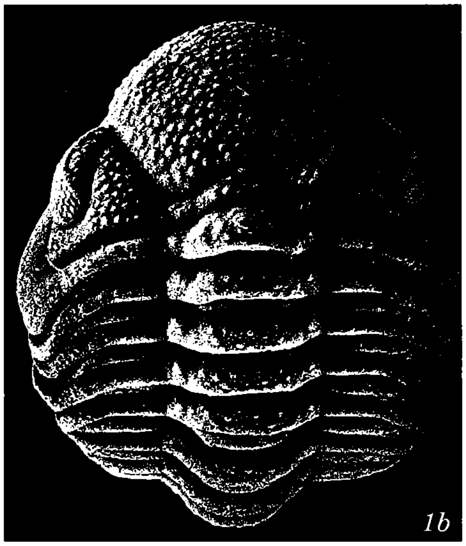
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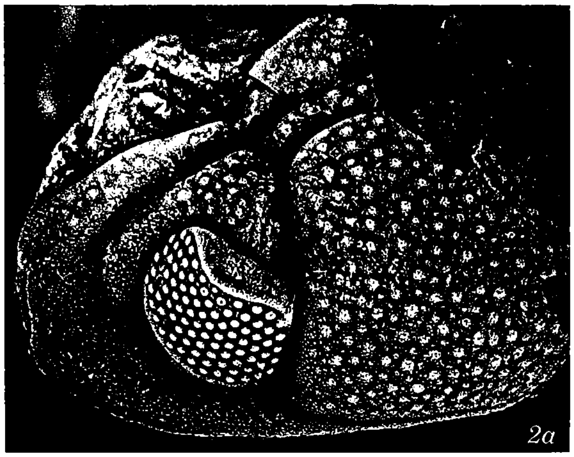
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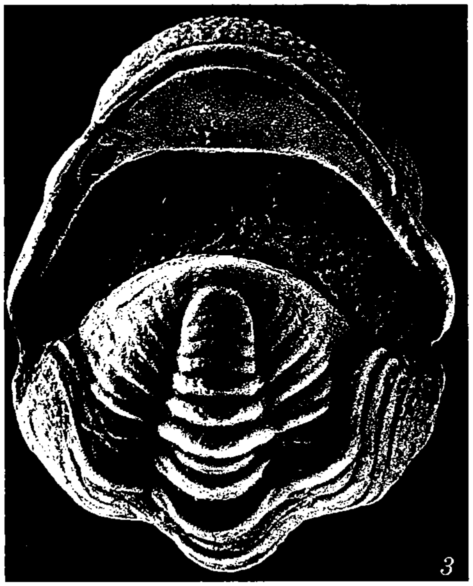
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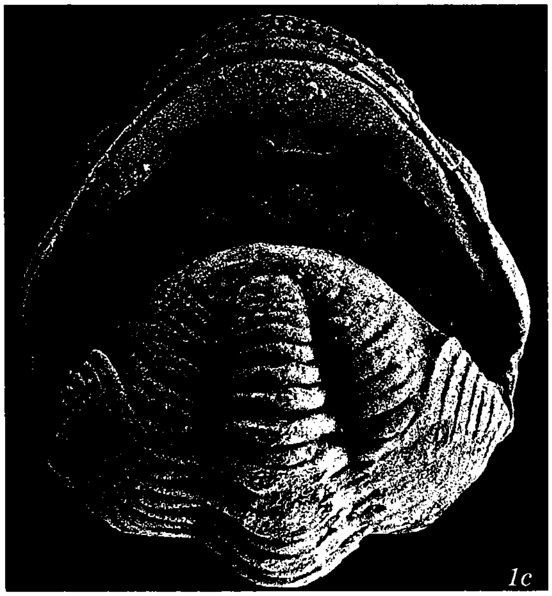

1c

Plate 8

Figures 1a-c. *Paciphacops (Paciphacops) raymondi* (Delo). Small-eyed morph; note shapes of pleural tips, muscle scars on pygidial axis, and inner and outer bands of pygidial doublure. Exoskeleton has been stripped from pygidium. OU 3426; *a, b,* ×2.25; *c,* ×3 approx. Haragan Formation, Old Hunton Townsite.

Figure 2. *Paciphacops (Paciphacops) raymondi* (Delo). Eye of small-eyed morph. USNM 208984B, ×9. Haragan Formation, Old Hunton Townsite.

Figure 3. *Paciphacops (Paciphacops) raymondi* (Delo). Ventral surface of dorsal exoskeleton of thorax and pygidium prepared by air-brasion. Small-eyed morph; note position of apodemes, long doublures on thoracic segments, and varied shapes of "stops" on thoracic doublures. OU 8272, ×5.9. Haragan Formation, White Mound.

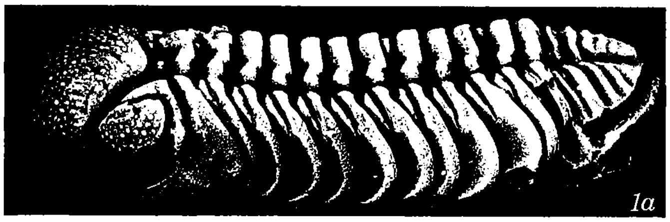
Figures 4a-c. *Paciphacops (Paciphacops) raymondi* (Delo). Hypostome excavated from beneath specimen shown in figure 1; dorsal, oblique, and ventral views. ×6.5.

Figure 5. *Paciphacops (Paciphacops) logani* (Hall). Hypostome of large-eyed morph from Clarksville, New York, with most of exoskeleton stripped away. YPM Collection, ×3.7.

Figure 6. *Phacops iowensis* Delo. Ventral view of holotype cephalon to show crushed hypostome. Note linear ornament on cephalic doublure and parts of hypostome as well as long posterior hypostomal border. Iowa State University Collection 9-266, ×5.5 approx.

Figure 7. *Paciphacops (Paciphacops) birdsongensis* (Delo). Ventral view of large-eyed morph showing hypostome. Specimen prepared with Airbrasive, but traces of granulation still visible. ANU 30589, ×3. Birdsong Shale, Big Sandy River, Tennessee.

Plate 8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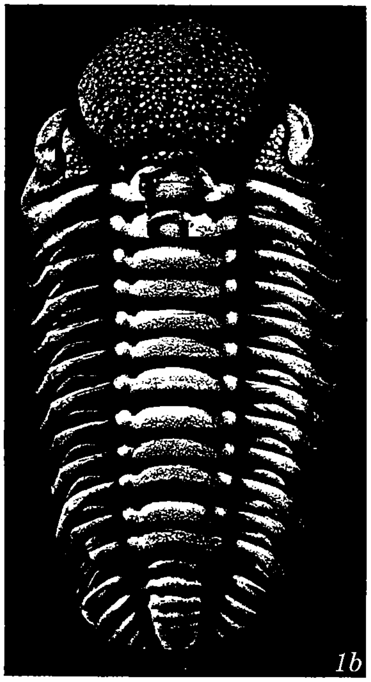
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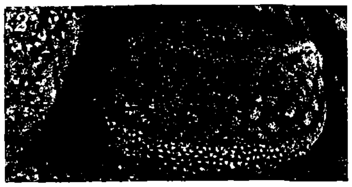
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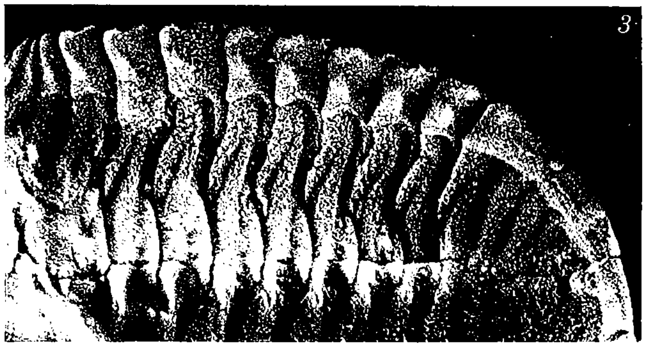
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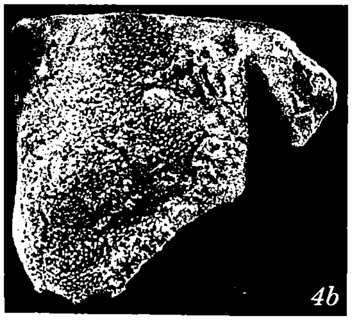
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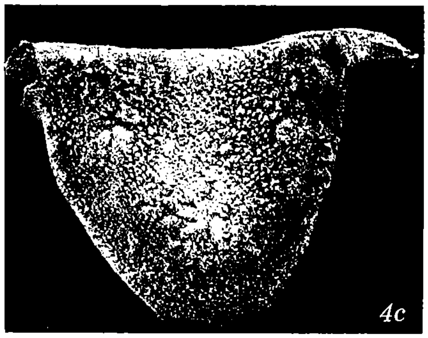
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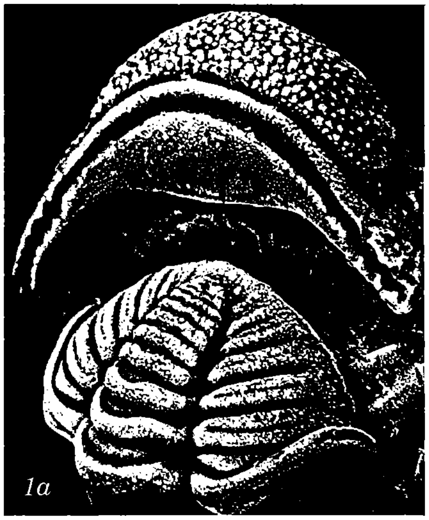
Plate 9

Figures 1a, b. *Paciphacops (Paciphacops) raymondi* (Delo). Small-eyed morph. ANU 30590, ×3.4. Haragan Formation, Old Hunton Townsite.

Figures 2, 3. *Paciphacops (Paciphacops) raymondi* (Delo). Cephalon and pygidium. OU 6817, ×4.3, and OU 8274, ×4. Haragan Formation, Old Hunton Townsite.

Figures 4a-d. *Paciphacops (Paciphacops) birdsongensis* Delo. Small-eyed morph. USNM 27850, ×3. Birdsong Shale, Big Sandy River, Tennessee.



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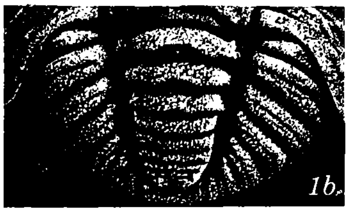

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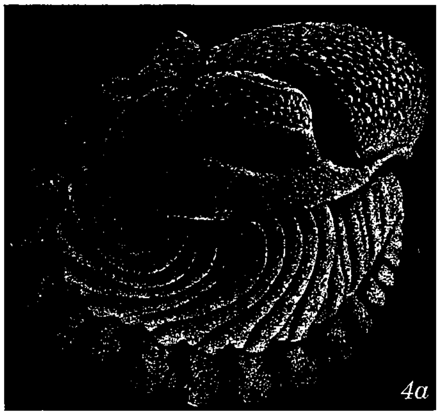

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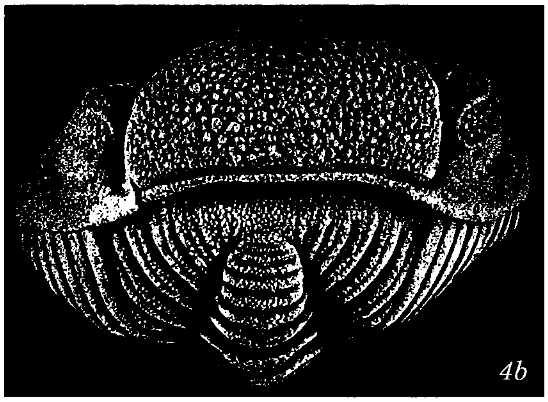

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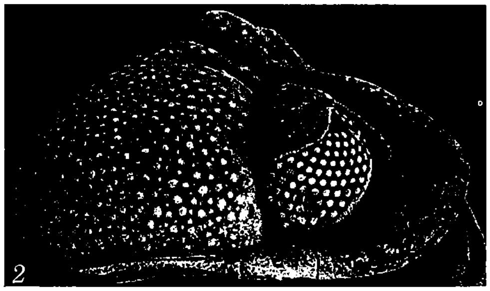

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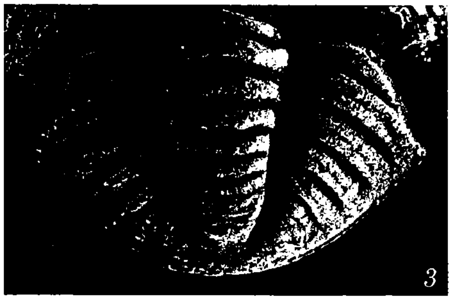

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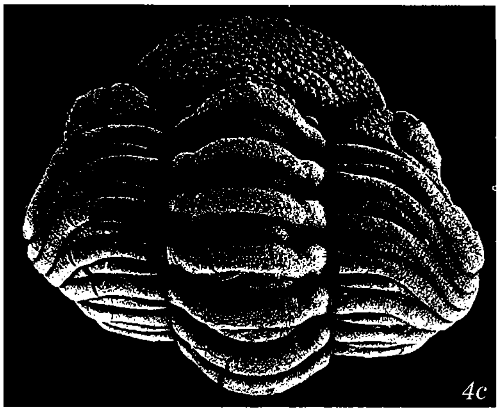

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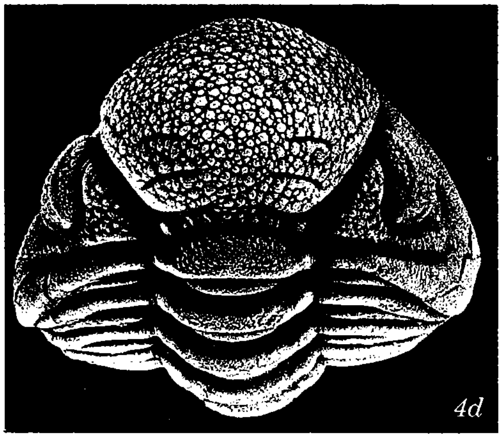


4d

Plate 10

All specimens *Paciphacops (Paciphacops) raymondi* (Delo), small-eyed morph from Haragan Formation.

Figures 1a, b. Almost complete specimen. USNM 183893, ×3.7. Nebo, Coal County.
Figure 2. Well-preserved thorax showing ornament. OU 6609, ×4.4. Old Hunton Townsite.
Figure 3. Four views of almost complete specimen. OU 7220, ×3.3. Old Hunton Townsite.

Plate 10

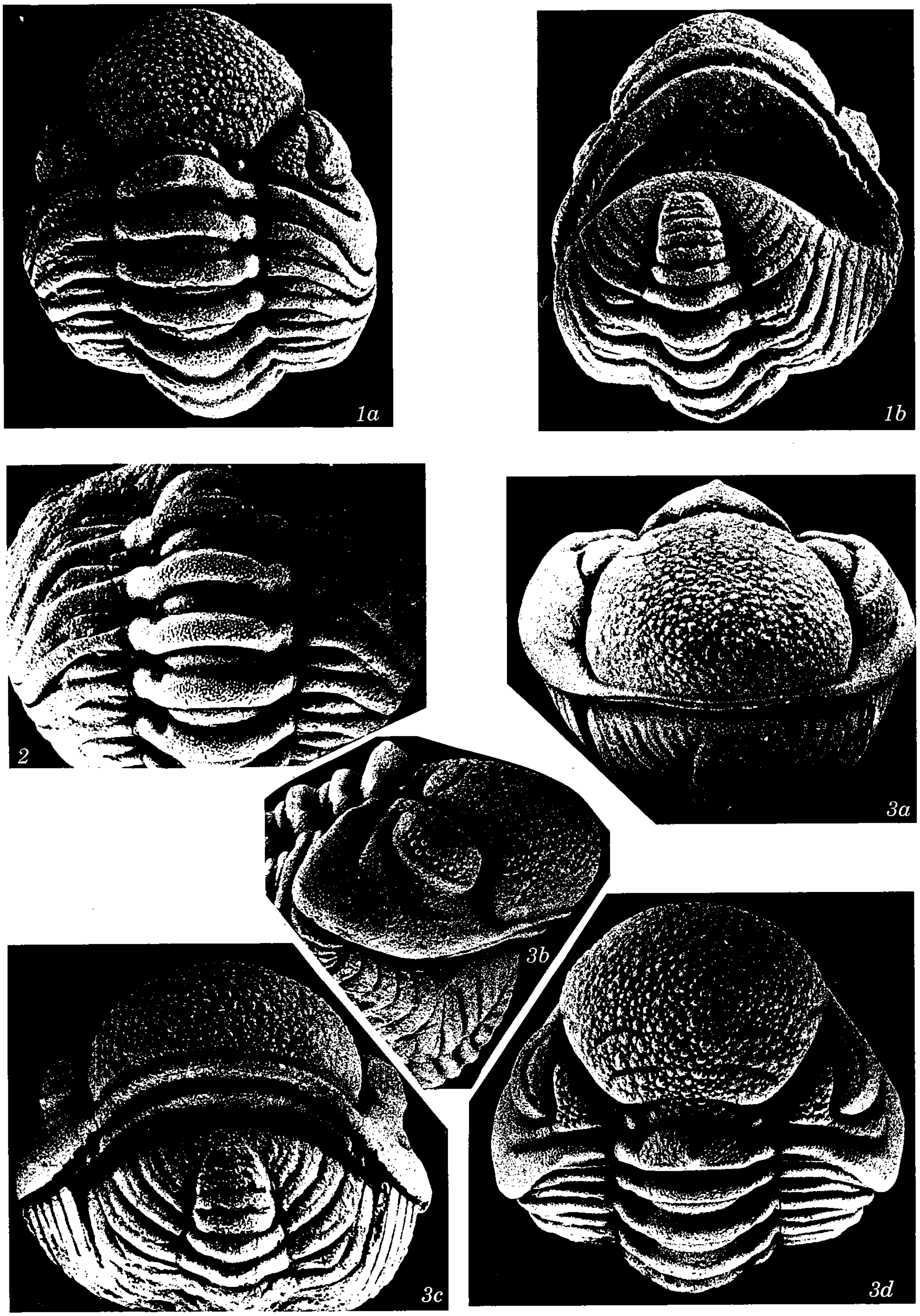
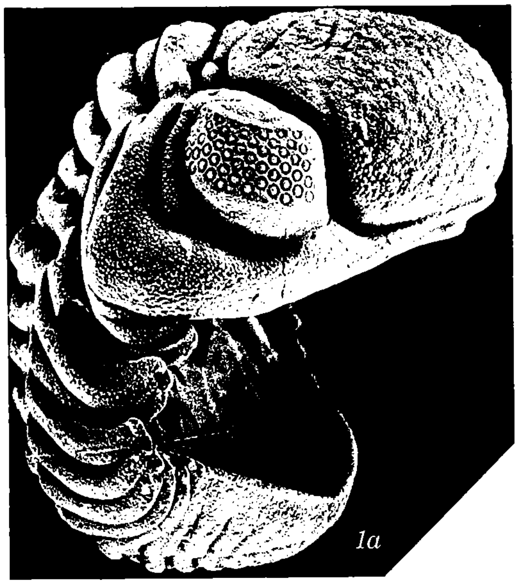


Plate 11

All specimens are *Paciphacops (Paciphacops) birdsongensis* (Delo), from Birdsong Shale, Steel Bridge over Big Sandy River, Tennessee.

Figures 1a-c. Three views of large-eyed morph. Note row of muscle scars around anterior border of cephalon. ANU 30588, ×3.5.
Figures 2a-d. Four views of intermediate morph. USNM 27849, ×2.9.



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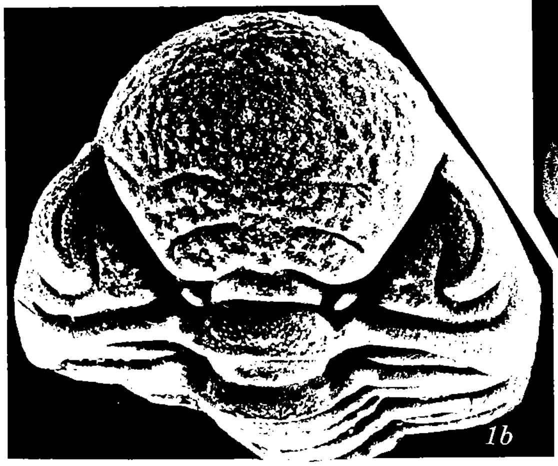

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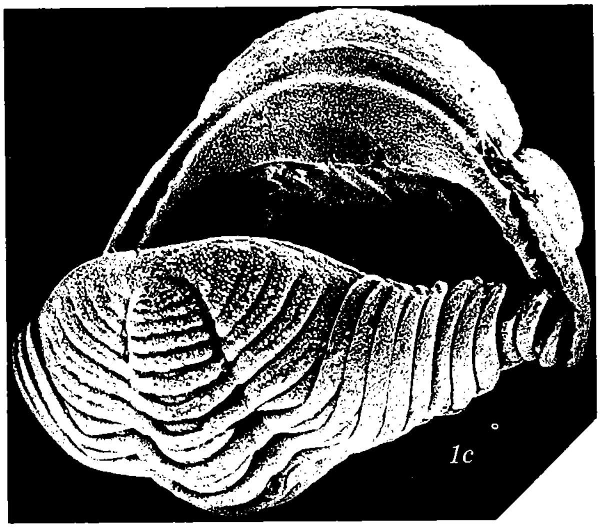

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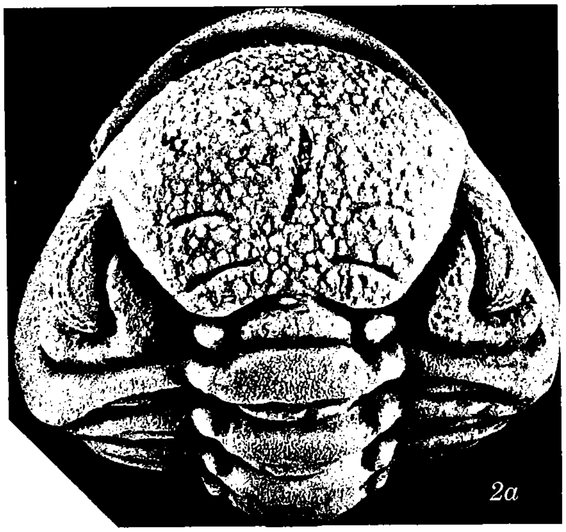

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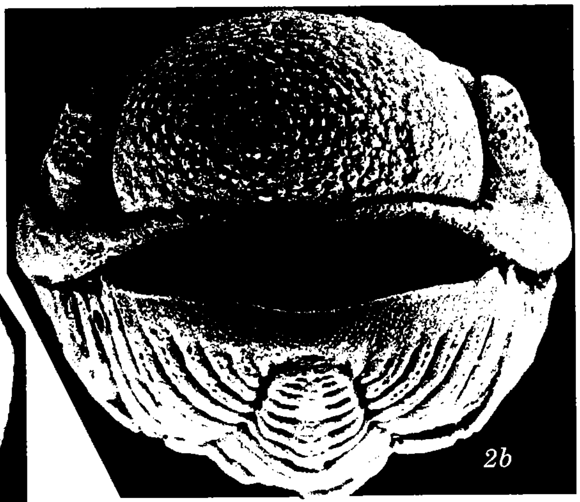

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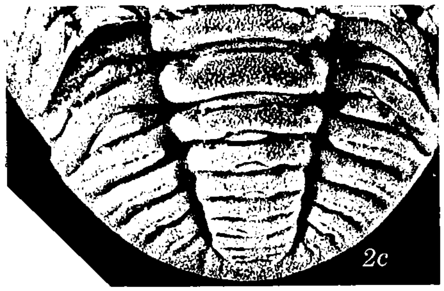

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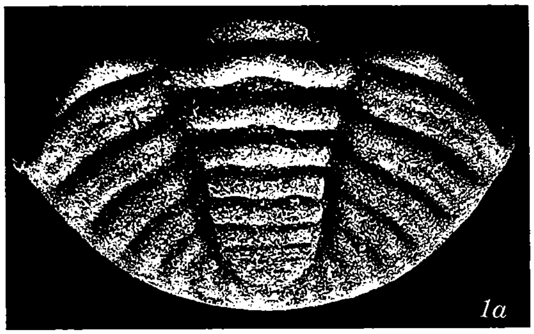
Plate 12

All specimens *Paciphacops (Paciphacops) logani* (Hall), from New Scotland Formation, Indian Ladder, New York. YPM (Beecher) Collection 6594.

Figures 1a-c. Dorsal, posterior, and lateral views of silicified pygidium. ×5.
Figure 2. Ventral view of silicified pygidium. ×5.
Figures 3a-c. Lateral, ventral, and dorsal views of silicified cephalon. ×3.
Figures 4a-c. Same, ×2.5.



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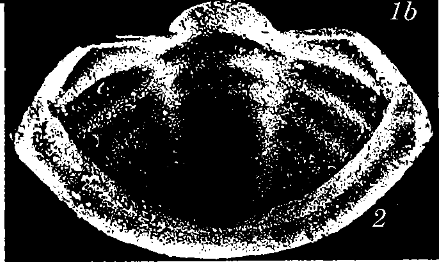

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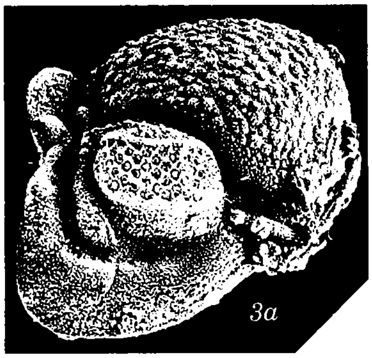

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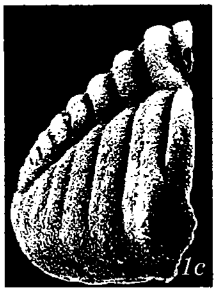

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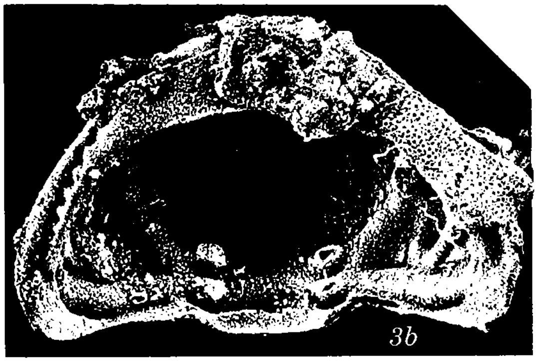

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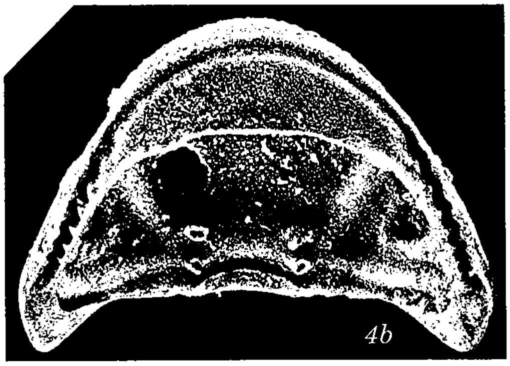

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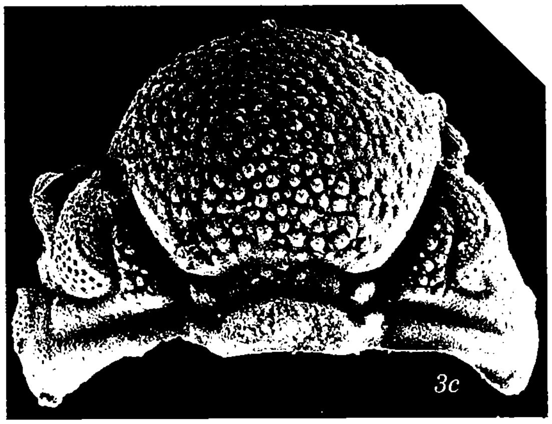

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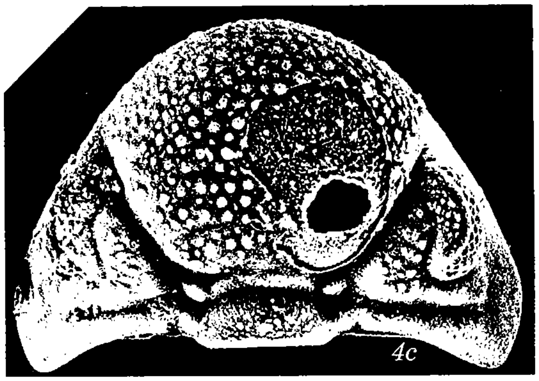


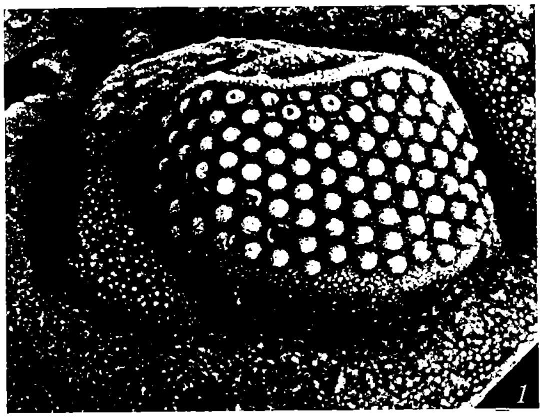
4c

Plate 13

Figures 1, 2. *Paciphacops (Paciphacops) raymondi* (Delo). Large- and small-eyed morphs. OU 8273, ×9, and OU 6814, ×11. Haragan Formation, locality M1—K.

Figures 3, 4. *Paciphacops (Paciphacops) logani* (Hall). Large- and small-eyed morphs. Figure 3 is from Clarksville, New York, and is ×10; figure 4 is from Indian Ladder, New York, and is ×9. Both in YPM Collection 6594.

Figures 5-7. *Paciphacops (Paciphacops) birdsongensis* (Delo). Large-, intermediate-, and small-eyed morphs, all from Steel Bridge, Big Sandy River. Figure 5, ANU 30588, ×9; figure 6, USNM 27849, ×9; figure 7, USNM 27850, ×9.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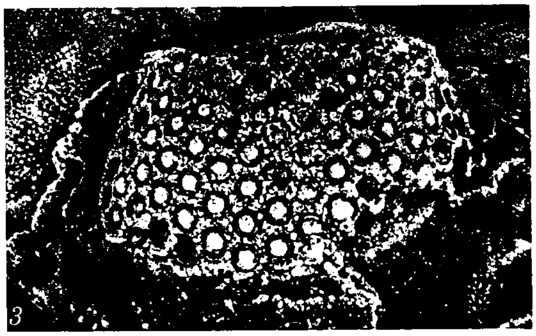
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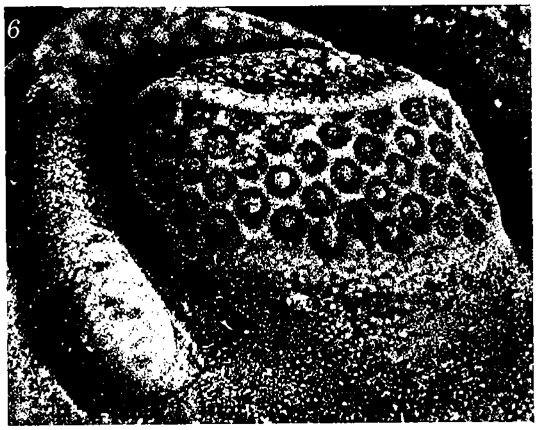
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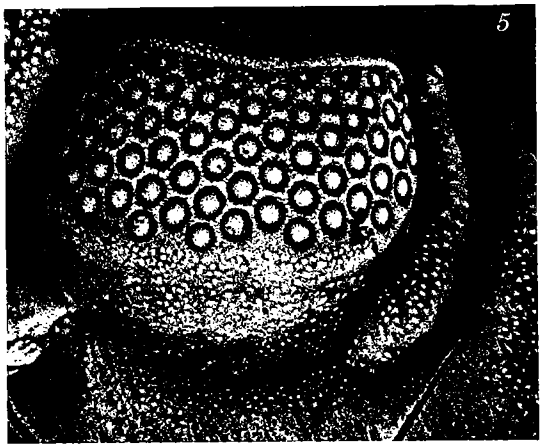
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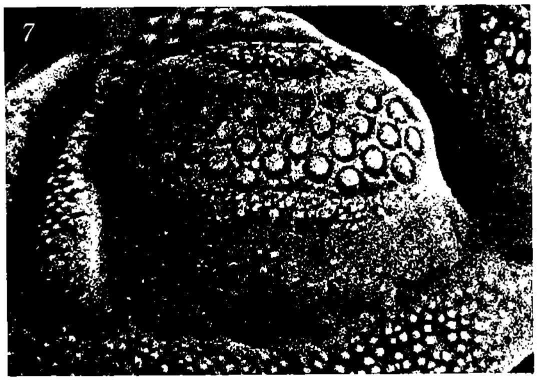
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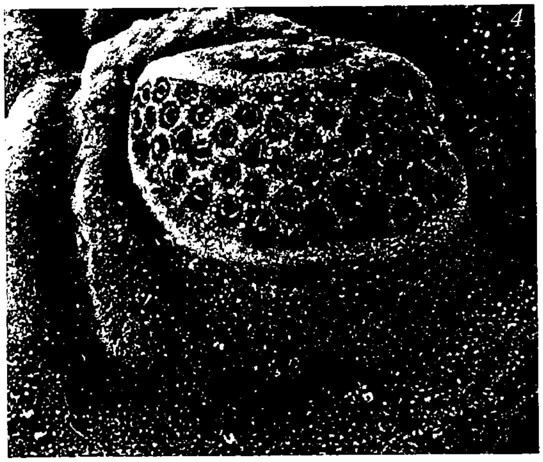
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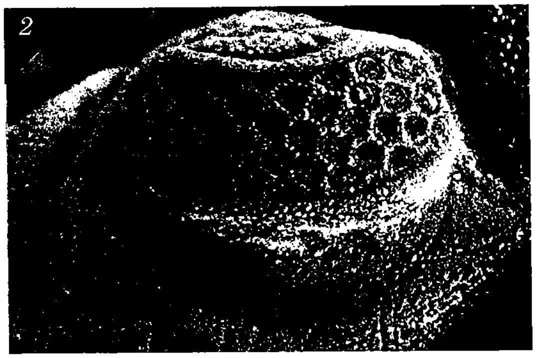
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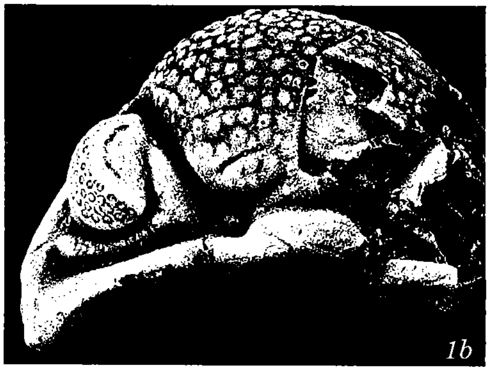
Plate 14

Figures 1a-c. *Paciphacops (Viaphacops),* new species. Posterior, dorsal, and lateral views of small-eyed specimen. Note perforations in tubercles. OU 7216, ×2.5. Frisco Formation, locality P9—R.

Figures 2a-f. *Paciphacops (Paciphacops) invius,* new species. Several views of holotype. Note weak sclera in eye of figure 2a, general absence of granulation of glabellar tubercles (which are perforated), distinct 1p lobe, and discrete granules on doublure in figure 2c. OU 7213; *a,* ×7; *b-e,* ×3; *f,* ×4.5. Fittstown Member, locality Ca1 (2)—V(2).


1a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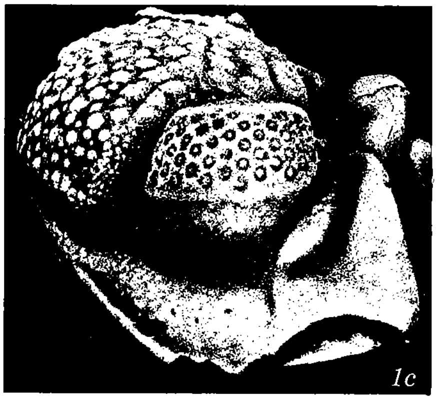
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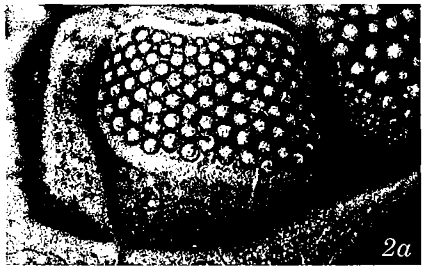
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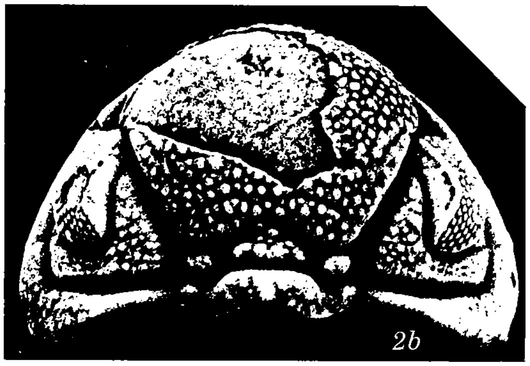
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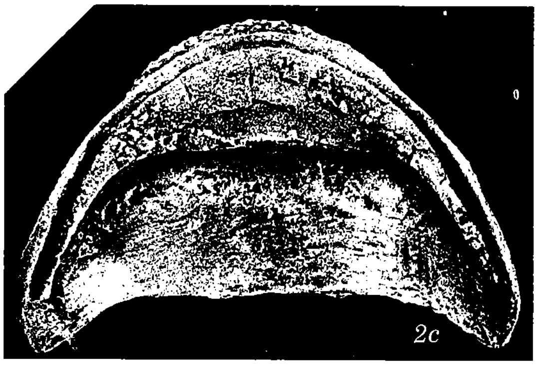

2c


2d


2f

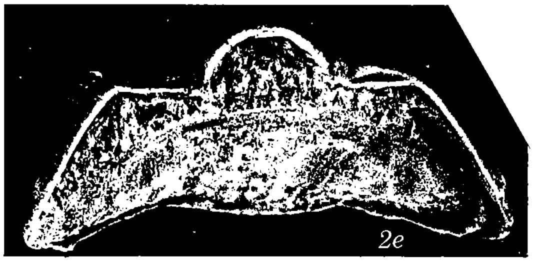

2e

Plate 15

Figures 1a-d. ?*Paciphacops (Paciphacops) invius,* new species. Probable specimen of small-eyed morph of this species. Glabellar ornament well preserved. OU 7212A; *a* and *c*, ×4; *b* and *d,* ×6. Fittstown Member, locality P3—GG.

Figures 2a, b. ?*Paciphacops (Paciphacops) invius,* new species. Probable specimen of small-eyed morph of this species. Note arrangement of granules on doublure. OU 7212B; *a,* ×3.3; *b,* ×5. Fittstown Member, locality P16.

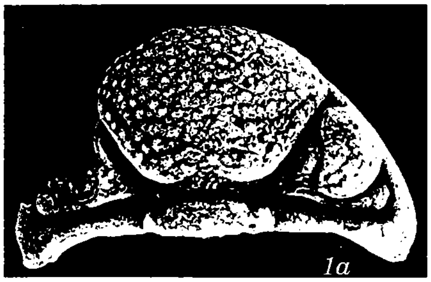
Figures 3a-c. *Paciphacops (Paciphacops)* cf. *P. birdsongensis* (Delo). Partly stripped individual. OU 7211, ×3. Fittstown Member, locality P3—GG.

Figures 4a, b. *Paciphacops (Viaphacops) cristata* cf. *P. bombifrons* (Hall). Specimen has most of exoskeleton removed. Note smooth flat tubercles on right side of glabella. OU 7215, ×2. Frisco Formation, Coal Creek, Pontotoc County.

Figures 5a, b. *Paciphacops (Paciphacops),* new species. Dorsal and ventral views of best preserved specimen. OU 8263, ×2.1. Frisco Formation, Canyon Creek Ranch.

Figure 6. *Paciphacops (Paciphacops),* new species. Best preserved eye. OU 2002, ×2.5. Frisco Formation, Canyon Creek Ranch.

Figures 7a, b. *Paciphacops (Paciphacops) invius,* new species. Dorsal views of pygidium. OU 7214, ×1.5. and 2.4. Fittstown Member, Buckhorn Ranch.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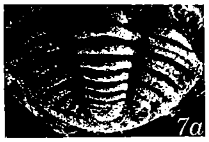
6


7b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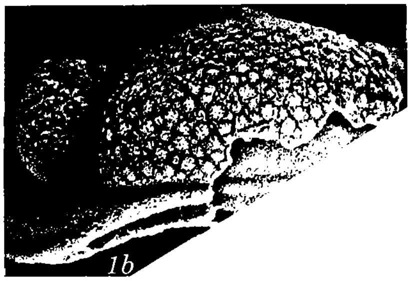
1d


5b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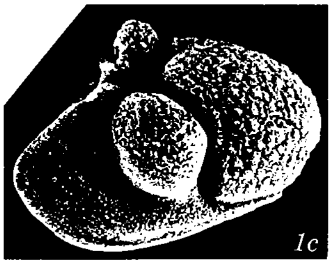
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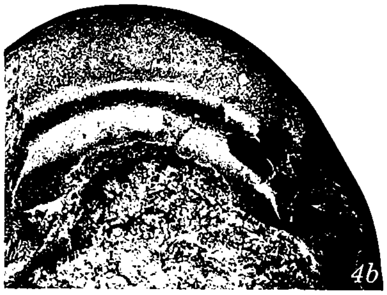
5a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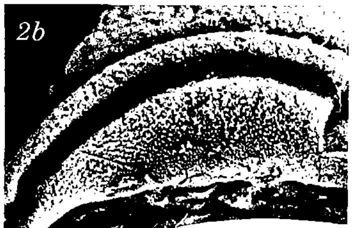
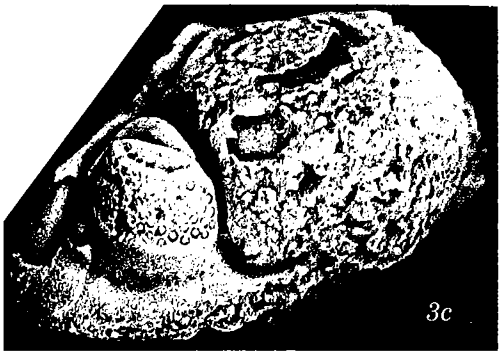

2b


2a


4a


3a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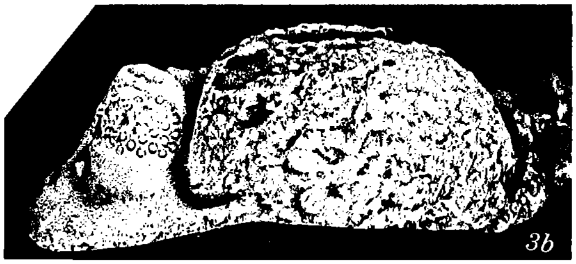
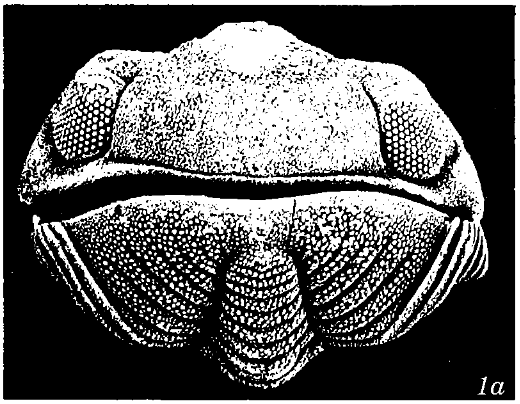

3b

Plate 16

All specimens *Reedops deckeri* Delo, from Haragan Formation.

Figures 1a-c. Three views of almost complete individual. OU 5378, ×2.5. Old Hunton Townsite.
Figure 2. Well-preserved specimen showing ornament of glabella and form of glabellar furrows. OU 3276, ×2.6. Old Hunton Townsite.
Figure 3. Oblique view of individual showing how pygidium overlaps anterior cephalic border on enrollment. USNM 208990, ×3.3. Vines dome.
Figure 4. Well-preserved eye showing thin sclera. OU 6559, ×5. Old Hunton Townsite.
Figure 5. Lateral view showing how thoracic pleural tips progressively change shape. OU 8271, ×3. White Mound.
Figure 6. One of small individuals with fine ornament from Vines dome, locality M1—J. OU 6556, ×3.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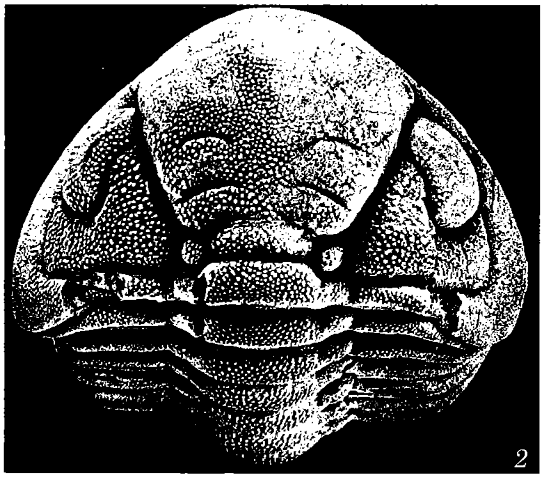
1b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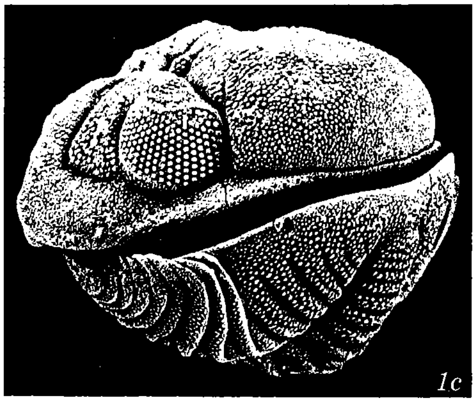
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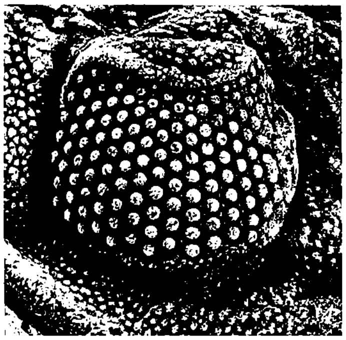

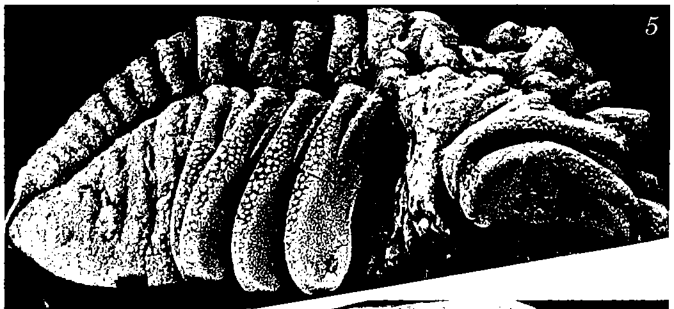
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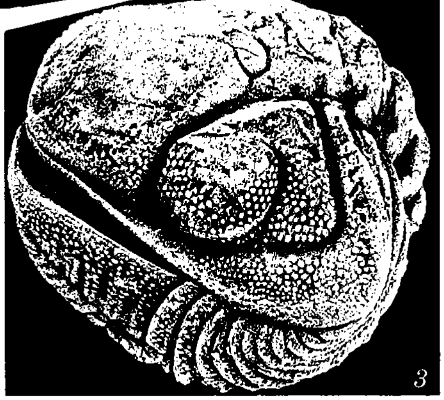
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Plate 17

Figures 1a, b. *Reedops sternbergi* (Hawle and Corda). Hypostome found in position beneath a cephalon. Palaeontological Museum, Oslo, 420, ×2.5. Hostim, Bohemia.

Figures 2-7. All specimens *Reedops deckeri* Delo and all from the Haragan Formation.

Figures 2, 3. *2a, b, c,* ventral, partial dorsal, and oblique views of small hypostome with complete posterior end. OU 6562A; *a* and *b*, ×2.75, and *c*, ×5. *3,* larger specimen with incomplete posterior. OU 6561, ×2.5. White Mound.

Figures 4a, b. Ventral views of two pygidia showing modification of doublure to fit over anterior edge of cephalon during enrollment. OU 6556A, and OU 6556B, ×2.5. Vines dome.

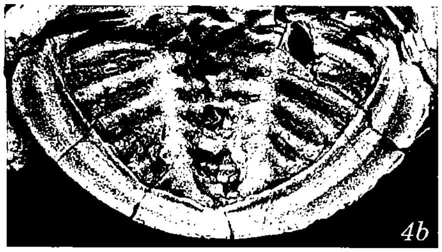
Figure 5. Part of well-preserved thorax. OU 6558B, ×2.5. White Mound.

Figures 6a, b. Two views of almost complete specimen. OU 6558A, ×2.6. White Mound.

Figure 7. Well-preserved thorax. Same specimen as plate 16, figure 2. OU 3276, ×2.6. Old Hunton Townsite.

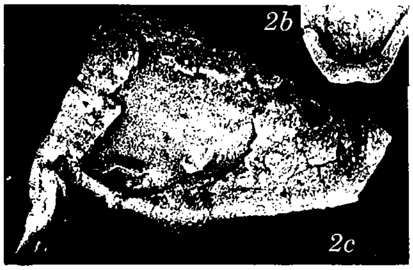
Plate 17


4a


4b


1b


2a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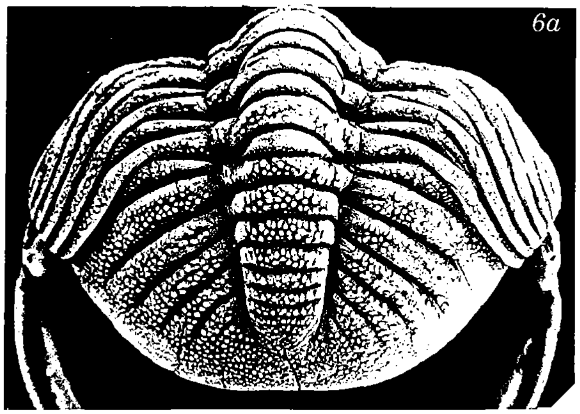
2c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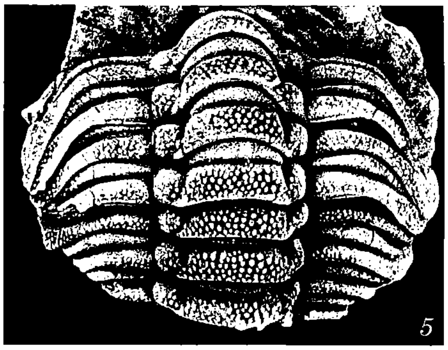
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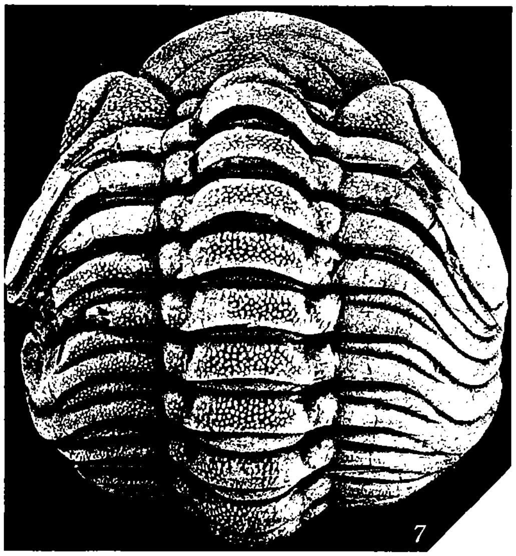
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6b

Plate 18

Figures 1a, b. *Huntonia (Neoprobolium) nasuta* (Conrad). Plaster cast of pygidium originally figured by Hall, 1861, plate 76, figure 7. NYSM 4347, ×2 and ×1. Helderbergs.

Figures 2-4. *Huntonia (Neoprobolium) nasuta* (Conrad). Plaster casts of three cephala, *3* in ventral view, and *2* and *4* in dorsal view. Figures 3 and 4 originally figured by Hall, 1861, plate 76, figures 3 and 2. NYSM 9848, 4345, and 4344, ×1, ×1, and ×1.2. Helderbergs.

Figure 5. *Huntonia (Neoprobolium) nasuta* (Conrad). Plaster cast of pygidial mold prepared to show doublure. Originally figured by Hall, 1861, plate 75, figure 2. NYSM 4342, ×1. Helderbergs.

Figure 6. *Huntonia (Huntonia) lingulifer* (Ulrich and Delo). Paratype cephalon figured by Delo, 1940, plate 3, figure 29. USNM Collection, ×2.5. Haragan Formation.

Plate 18

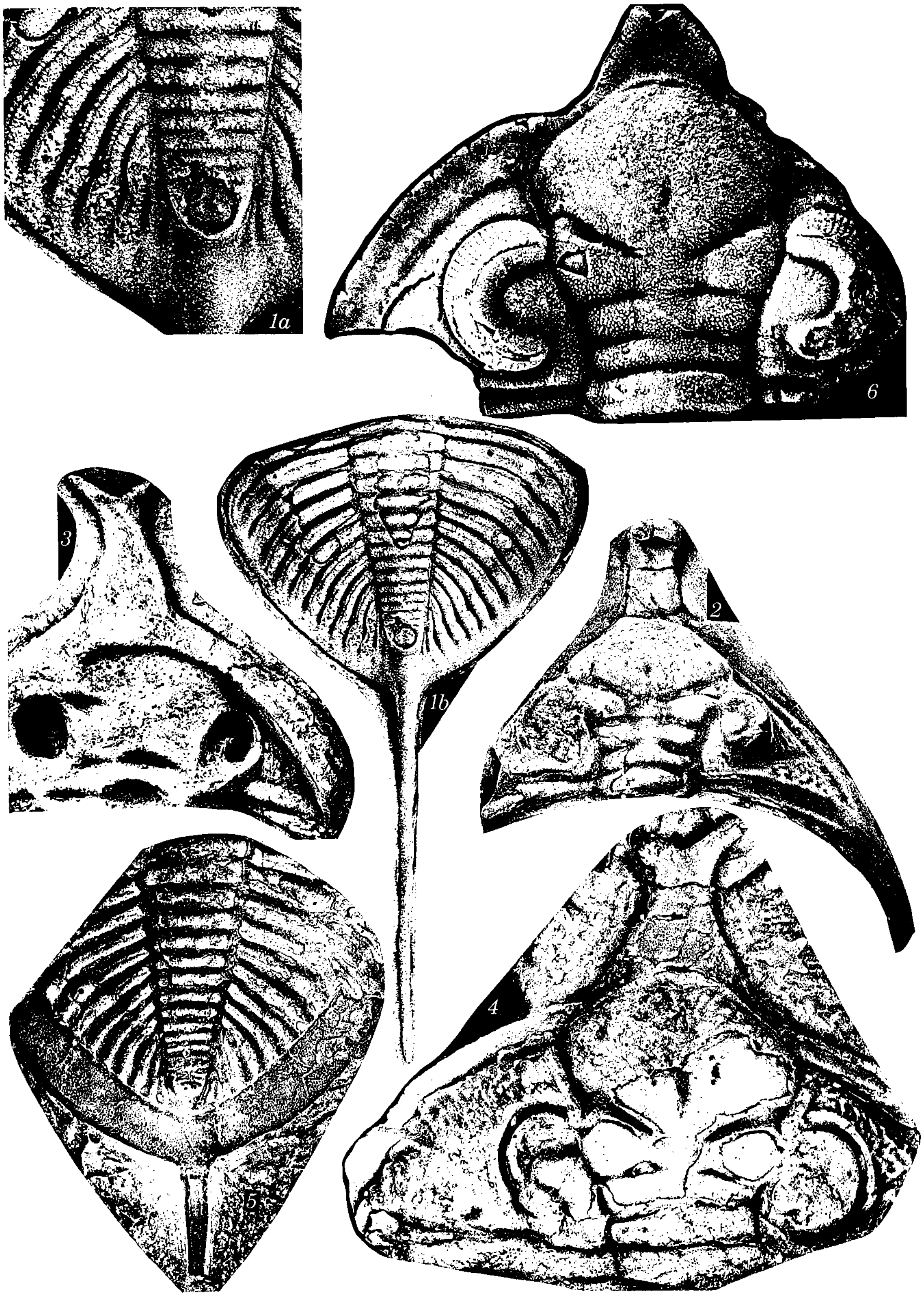

Plate 19

Figures 1-3. *Huntonia (Huntonia) purduei purduei* (Dunbar). *1, 2,* photographs of eyes of specimen figured on plate 24, figure 8, with various parts of lenses preserved in silica. USNM 143113B, ×15. *3,* specimen with most of lenses replaced by silica. USNM 144308B, ×40. Symbols as in text. Both specimens from Ross Limestone, Pickwick Dam, Tennessee.

Figure 4. *Huntonia (Huntonia) lingulifer* (Ulrich and Delo). Cast of holotype. USNM 111557, ×1.5. Haragan Formation, Atoka quadrangle.

Figures 5a-c. *Huntonia (Huntonia) lingulifer* (Ulrich and Delo). *a, b,* ventral and dorsal views of specimen with well-preserved surface detail; *c,* enlargement of part of axis. OU 6603; *a,* ×1.7; *b,* ×1.5; *c,* ×2. Haragan Formation, northeast of Bromide.

Figure 6. *Huntonia (Huntonia) oklahomae* (Richardson). Hypostome; right posterior extremity has had surface destroyed and replaced by plaster of paris to correspond with template provided by doublure. OU 6578, ×3. Haragan Formation, Old Hunton Townsite.

Figure 7. *Huntonia (Huntonia) purduei purduei* (Dunbar). Well-preserved pygidium of Type A. See also plate 25, figure 4. OU 6598, ×1.6. Haragan Formation, northeast of Bromide.

Figure 8. *Reedops bronni* (Barrande). Note shapes of thoracic pleural tips. MCZ Collection, ×1.3. Tetin, Bohemia.

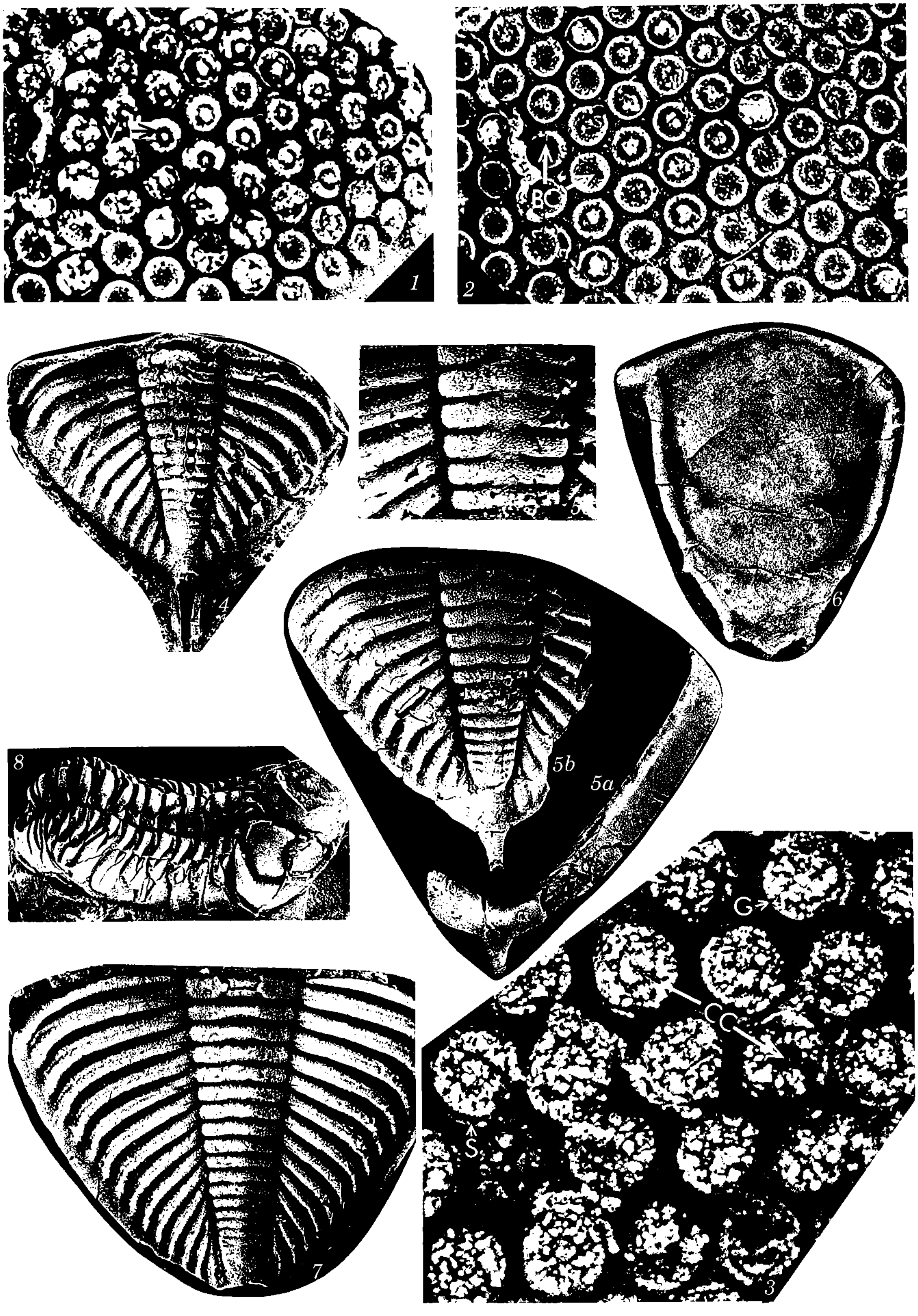
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Plate 20

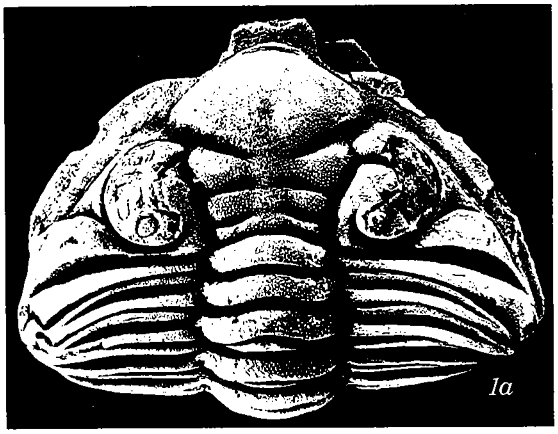
All specimens *Huntonia (Huntonia) lingulifer* (Ulrich and Delo), from Haragan Formation.

Figures 1a, b. Enrolled specimen. Note doublure of pygidium on right of broken anterior cephalic process. OU 3430, ×2 and ×3.3. Near Bromide.

Figures 2a, b. Part of thorax and pygidium, with enlargement to show muscle insertions and ornament. Note long pleural tips on posterior thoracic segments. OU 7209, ×1.5 and ×5. Old Hunton Townsite.

Figure 3. Incomplete enrolled specimen. Tip of anterior process is complete. USNM 208986B, ×2. Old Hunton Townsite.

Figures 4a, b. Incomplete enrolled specimen. OU 6591, ×3 and ×2. Old Hunton Townsite.



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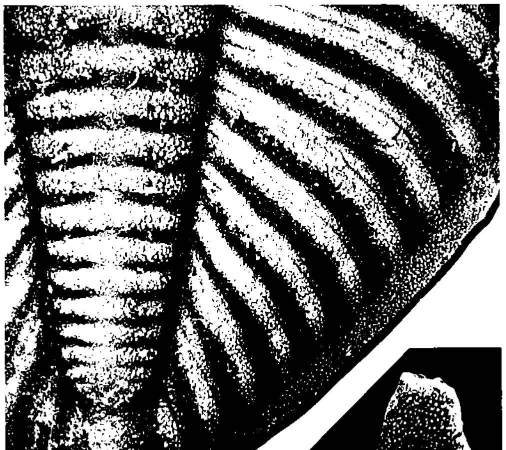
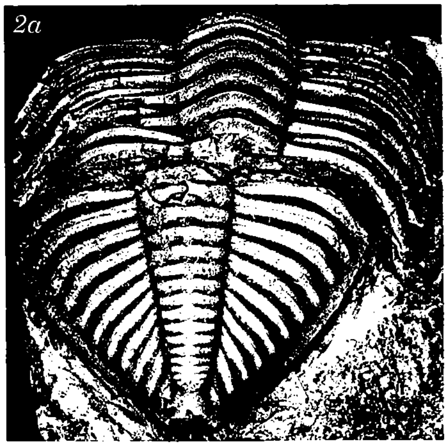


2b

1b

3

4a



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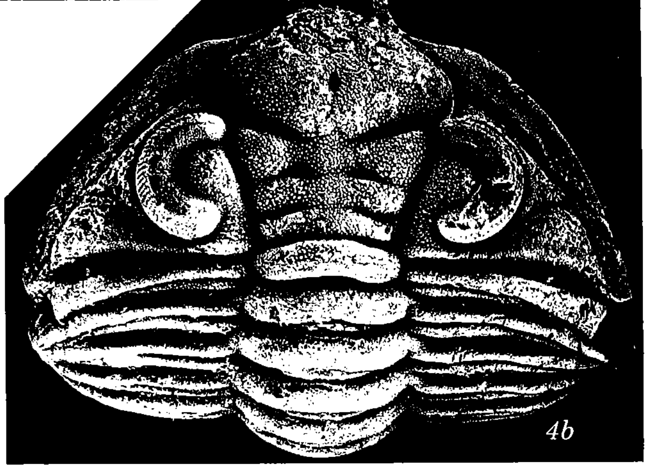


4b

Plate 21

All specimens *Huntonia (Huntonia) huntonensis* (Ulrich and Delo), from Haragan Formation.

Figures 1a, b. Enlargements of anterior and posterior parts of two pygidia to show details of ornament. Note particularly muscle insertions on rings in *a*; OU 6505, ×2.4, and USNM 208989C, ×3.6. Coal Creek, Murray County, and Old Hunton Townsite.

Figures 2a, b. Hypostome and incomplete cephalon. Note muscle-insertion spots on hypostome and characteristic wide doublure on right side of cephalon; OU 6582, ×3 and ×1.6. Old Hunton Townsite.

Figures 3a-d. Ventral, dorsal, anterior, and partial ventral views of specimen with almost complete anterior process. Tip of process chipped on each side. Dorsal surface of eyes and anterior glabellar lobe badly worn. OU 3410; *a-c,* ×1.5, and *d,* ×4. Old Hunton Townsite.

Figure 4. Enlargement of part of glabella showing characteristic ornament. OU 6581, ×4. Old Hunton Townsite.

Figure 5. Anterior part of cephalon with broken anterior process, well-preserved facial suture, and clear muscle insertions into anterior glabellar lobe. OU 8270, ×2. Old Hunton Townsite.

Plate 21

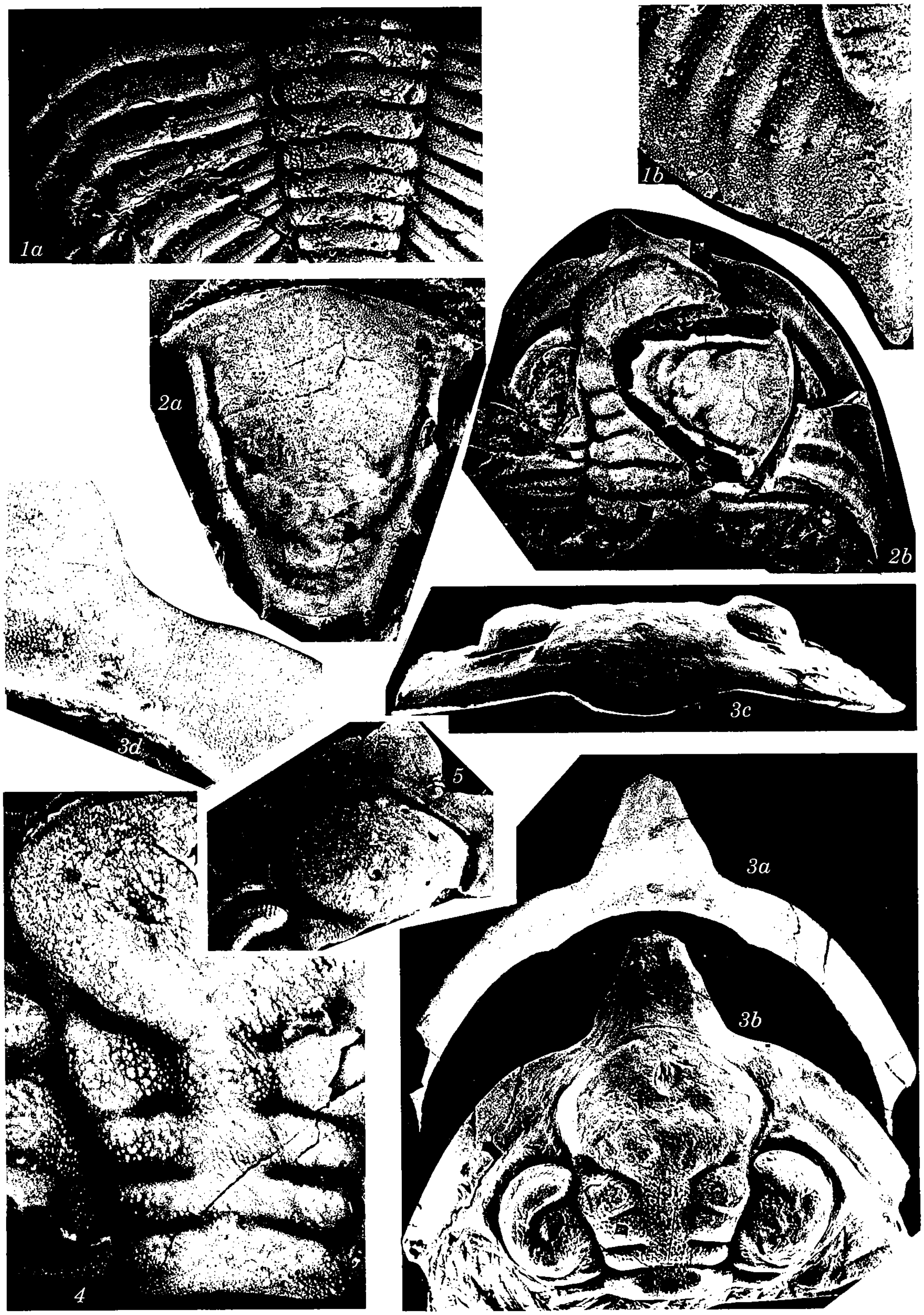
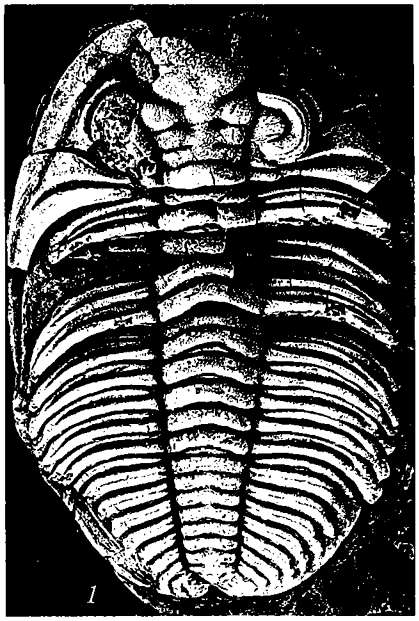


Plate 22

All specimens *Huntonia (Huntonia) huntonensis* (Ulrich and Delo), from Haragan Formation.

Figure 1. Almost complete specimen with teratological pygidium. USNM 208989A, ×1.5. Old Hunton Townsite.
Figure 2. Cephalon prepared to show wide, flat doublure. OU 6581, ×2. Old Hunton Townsite.
Figures, 3, 6. Holotype and paratype pygidia. USNM 79036 and USNM 11572, both ×1.5. Atoka quadrangle. (See Delo, 1940, pl. 3, figs. 26, 28.)
Figures 4a, b. Dorsal view of Type-A pygidium, and ventral view of its doublure. USNM 208989B, ×1.5. Old Hunton Townsite.
Figures 5a, b. Same. USNM 208989C, ×1.5. Old Hunton Townsite.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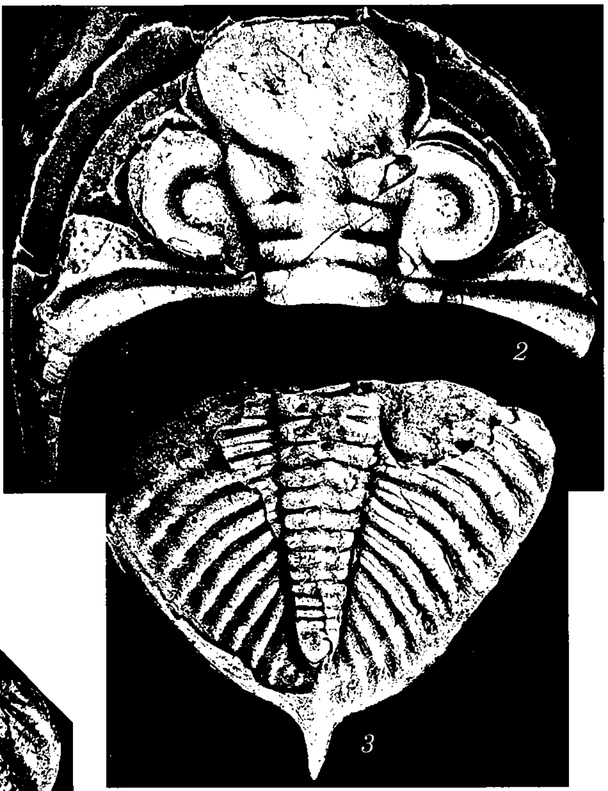
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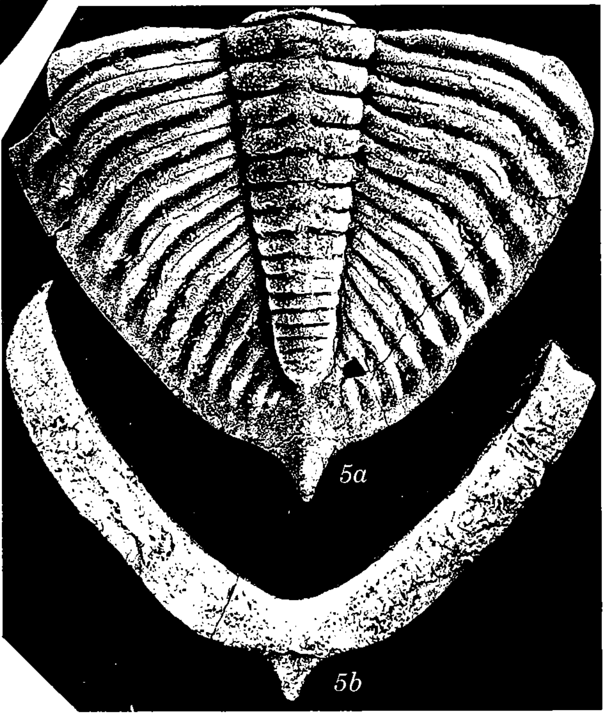
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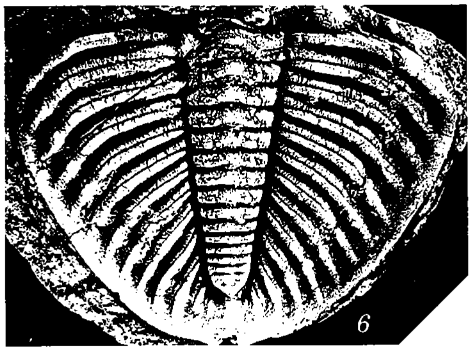
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Plate 23

All specimens *Huntonia (Huntonia) oklahomae* (Richardson), from Haragan Formation.

Figures 1a, b. Dorsal view of cephalon, with anterior process broken. ANU 14247, ×1.5. Old Hunton Townsite.

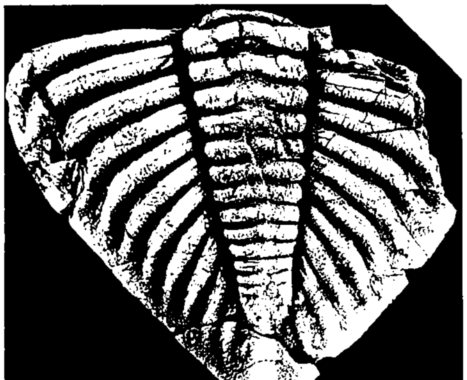
Figures 2a, b. Dorsal and ventral views of fragmentary pygidia. OU 6597, ×1.5, and unnumbered USNM, ×2.5. Old Hunton Townsite.

Figures 3a-c. *a, b,* dorsal and ventral views of unusually transverse pygidium; *c,* enlargement of posterior part to show ornament. OU 6604; *a, b,* ×1.5; *c,* ×3. Old Hunton Townsite.

Figures 4a, b. Dorsal and ventral views of normal pygidium. OU 6604, ×1.5. Old Hunton Townsite.

Figure 5. Ventral view of pygidium with spine broken, USNM 208988, ×2. Old Hunton Townsite.

Figure 6. Dorso-lateral view of pygidium showing normal angle of spine. OU 6600, ×2.5. Old Hunton Townsite.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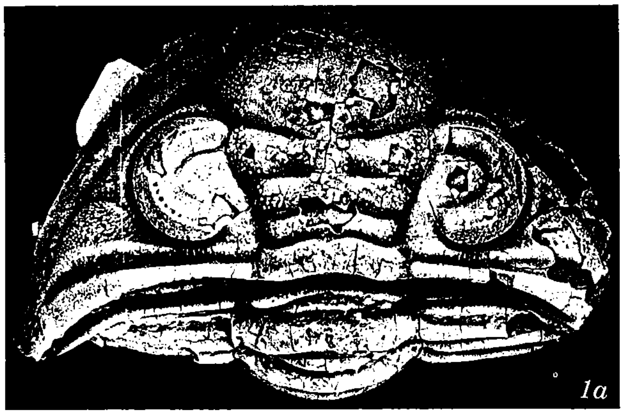
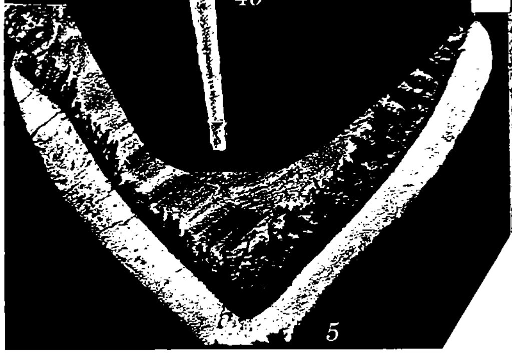

1a


2a


4b


3c


2b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3a

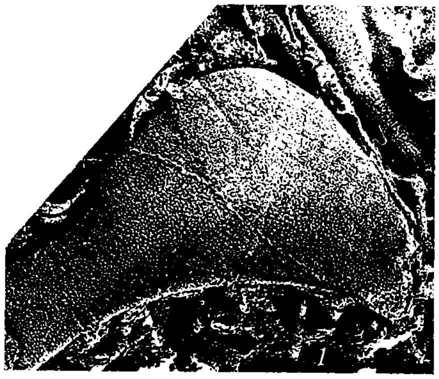

3b


1b

Plate 24

Huntonia (Huntonia) purduei purduei (Dunbar). All specimens from Ross Limestone, Pickwick Dam, Tennessee.

Figure 1. Latex cast of dorsal surface of anterior cephalic process and part of thoracic pleura. USNM 144308B, ×2.5.
Figure 2. Internal mold of hypostome. USNM 144308C, ×3.
Figures 3, 7, 9. Latex casts of anterior glabellar lobe, free cheek, and part of genal region. *3, 9,* USNM 114308B, ×3.5 and ×2.5; *7,* 208982D, ×3.
Figures 4, 5. Internal molds of Type-B and Type-C pygidium. USNM 144308A and 143113A, ×1.6 and ×1.0.
Figure 6. Latex cast of posterior of Type-A pygidium. USNM 144308B, ×2.4.
Figure 8. Internal mold of almost complete cephalon. USNM 143113B, ×1.3.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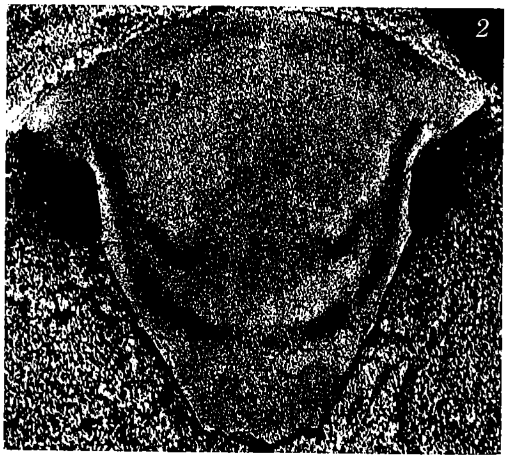
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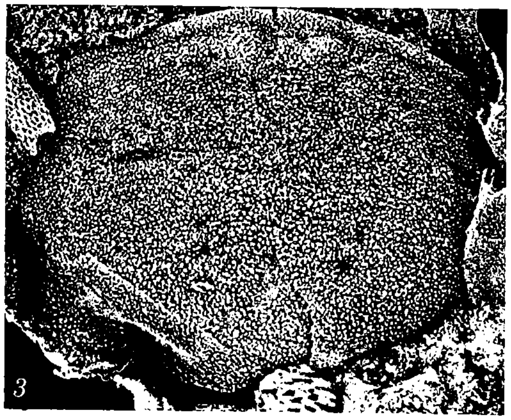
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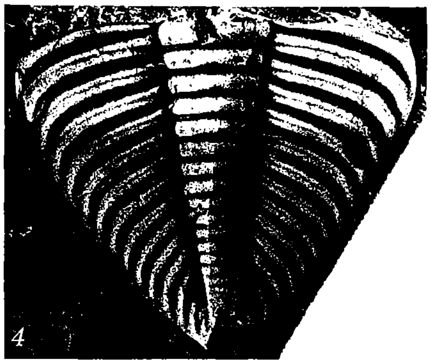
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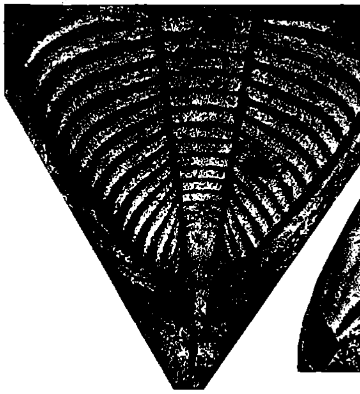
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Plate 25

All specimens *Huntonia (Huntonia) purduei purduei* (Dunbar).

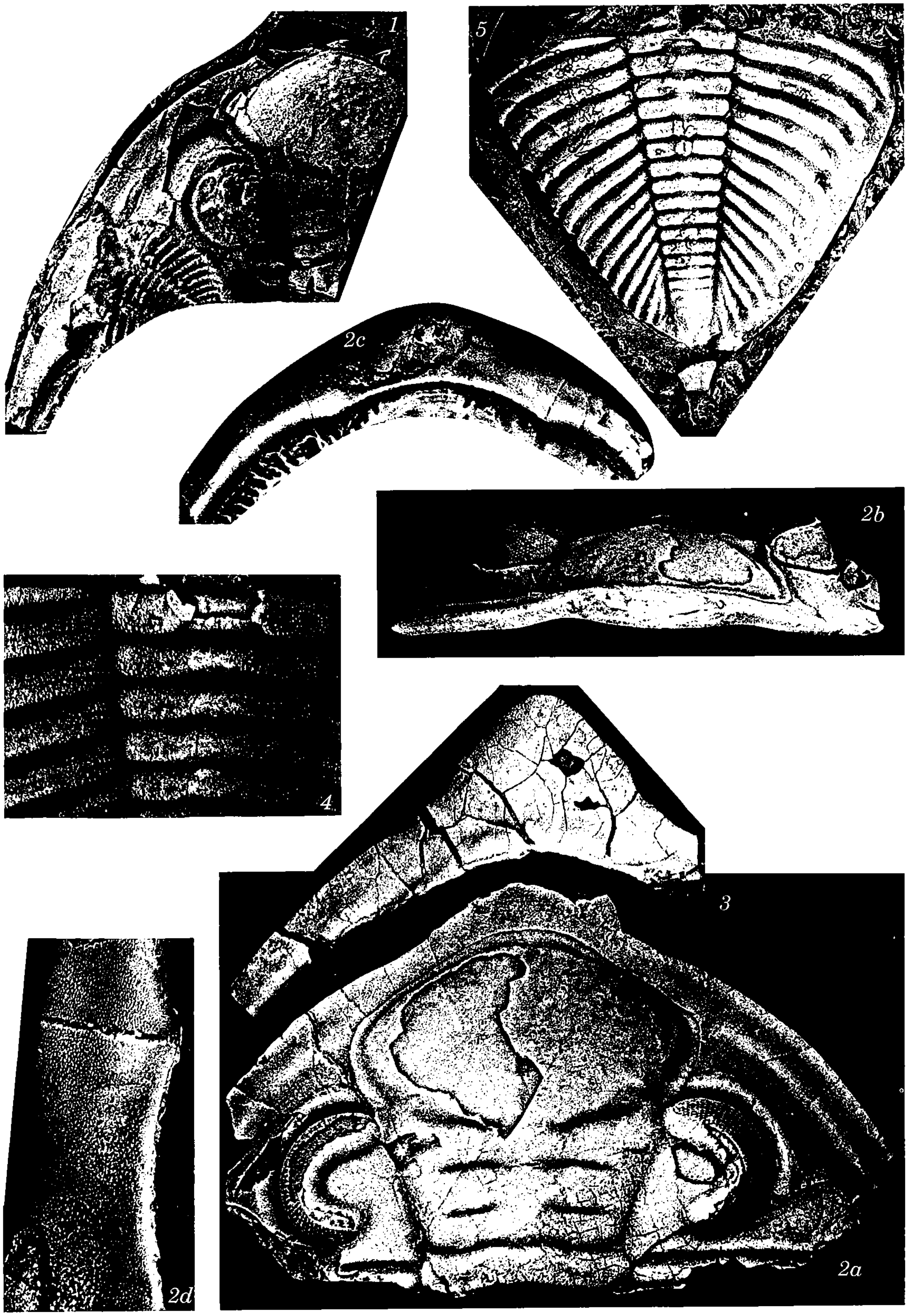
Figure 1. Partly stripped cephalon showing muscle insertions into anterior lobe and long (incomplete), slender genal spine. OU 8289, ×1.2. Haragan Formation, locality C2—J.

Figures 2a-d. Best preserved Haragan specimen of species. *a,* dorsal, *b,* anterior; *c,* doublure, and *d,* enlarged part of doublure. Anterior process broken. OU 6573, ×1.3, ×1, and ×1. Haragan Formation, Old Hunton Townsite.

Figure 3. Ventral view of part of cephalic doublure and complete anterior process. OU 8291, ×1.5. Haragan Formation, locality C2—I.

Figure 4. Enlargement of part of pygidium shown on plate 19, figure 7. Note muscle-insertion areas into axial rings. OU 6598, ×3. Haragan Formation, locality C2—H.

Figure 5. Internal mold of pygidium with doublure exposed on left and complete terminal spine. USNM 143113D, ×1.1. Ross Limestone, Pickwick Dam, Tennessee.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2c
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2d

Plate 26

All specimens *Huntonia (Huntonia) purduei fittstownensis,* new subspecies, from Fittstown Member, locality P16.

Figures 1, 2. Two glabellae showing ornament and distortion owing to muscle insertions into anterior lobe. OU 7196A and 7205B, ×2.2 and ×1.5.
Figures 3a-c. Type-A pygidium showing general form, ornament, and short terminal spine with ornamented doublure. OU 7206, ×2.75, ×1, and ×2.75.
Figures 4, 6. Testiferous specimen and internal mold of Type-C pygidia. Note muscle insertions on rings of figure 6. OU 7207A and 7203A, both ×1.5.
Figure 5. Partial internal mold of Type-A pygidium showing form of doublure. OU 7204, ×1.
Figure 7. Incomplete hypostome. OU 7196B, ×1.9.


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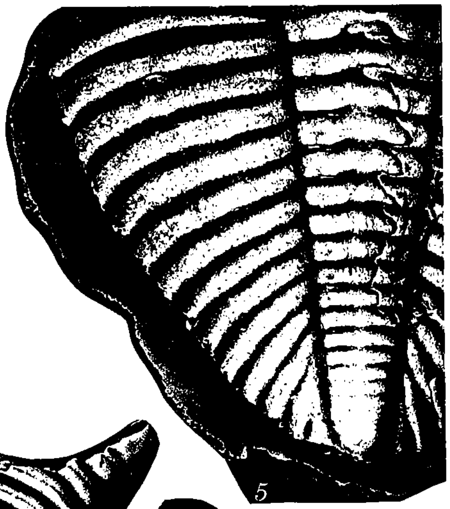
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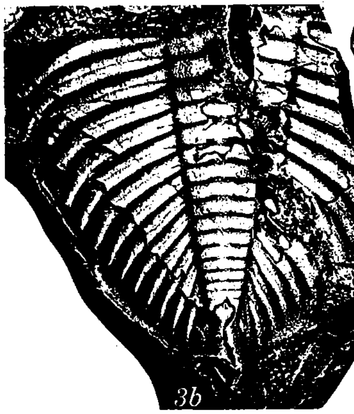
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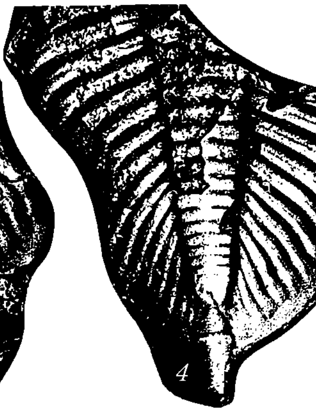
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6


3c


7

Plate 27

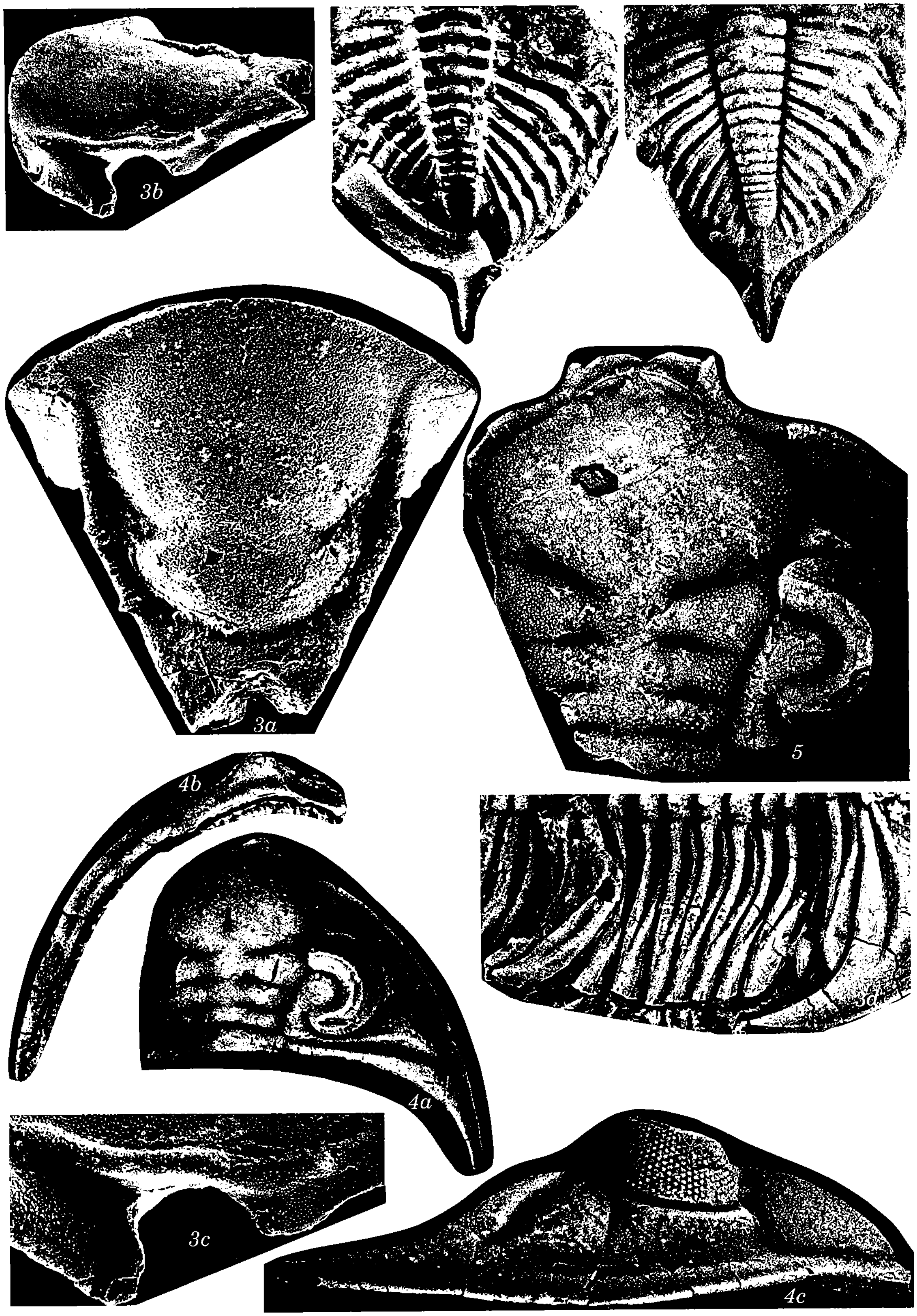
All specimens *Huntonia (Huntonia)* new form, and from Haragan Formation.

Figures 1, 2. An exterior with part of doublure and spine preserved, and latex cast of exterior of pygidium. OU 6583, ×1.6, and USNM 208987, ×1.4.

Figures 3a-d. *a-c,* three views of hypostome the posterior extremity of which was destroyed in preparation. *d,* lateral of dorsal exoskeleton of same individual. OU 3443; *a,* ×4; *b,* ×2.8; *c,* ×6; *d,* ×1.3. Old Hunton Townsite.

Figures 4a-c. Cephalon that probably belongs to this form. OU 6583; *a, b,* ×1.4; *c,* ×2.3. Old Hunton Townsite.

Figure 5. Enlargement of fragmentary cephalon showing ornament. OU 8275, ×2.4. Northeast of Bromide.


3b
2
3a
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4b
5a
4a
3c
4c

Plate 28

Figures 1a, b. Dalmanitacea, genus and species undet. Fragmentary pygidium. OU 6594Z, ×2 and ×1. Frisco Formation, southwest of St. Clair Lime Quarry.

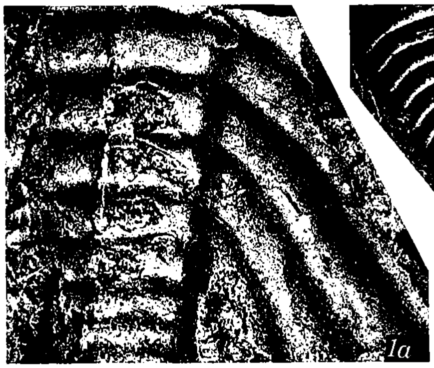
Figure 2. *Huntonia (Prosocephalus) xylabion,* new species. Paratype pygidium with most of exoskeleton removed. OU 6542, ×2. Fittstown member, locality Ca1 (2)—V(2).

Figure 3a-c. *Huntonia (Prosocephalus) xylabion,* new species. *a, b,* paratype pygidium in dorsal and anterodorsal views. *c,* latex cast of posterior of same. Note exposed doublure on right posterior of *a*. OU 6545; *a, b,* ×2.2; *c,* ×5. Fittstown member, locality J11—L.

Figures 4a, b. *Huntonia (Prosocephalus) xylabion,* new species. Dorsal and anterodorsal views of holotype cephalon. Note muscle insertions into anterior glabellar lobe. OU 6546, ×2.7. Fittstown member, locality P11—A.

Figure 5. *Odontochile syncrama,* new species. Holotype pygidium. OU 7197, ×1.5. Fittstown Member, locality P16.

Plate 28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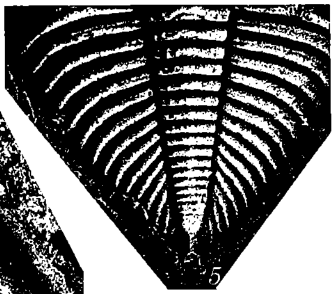
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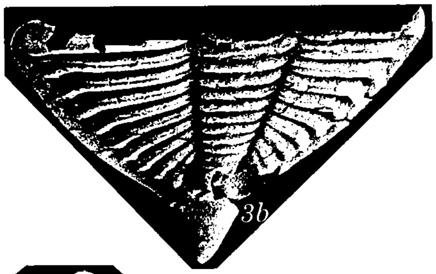
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1b


4a


3c

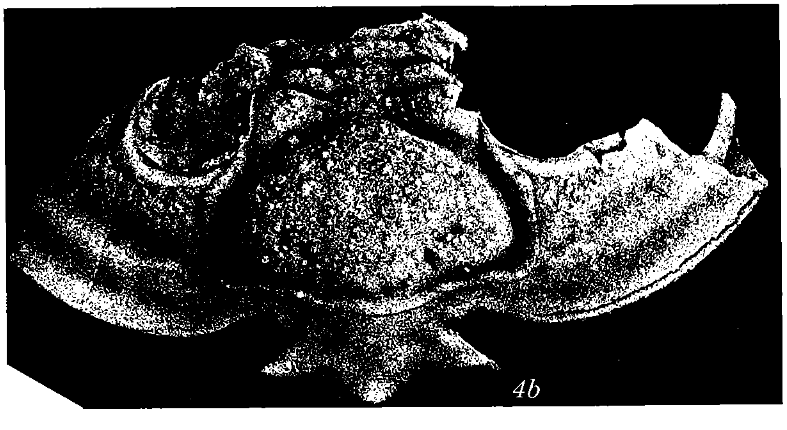

4b

Plate 29

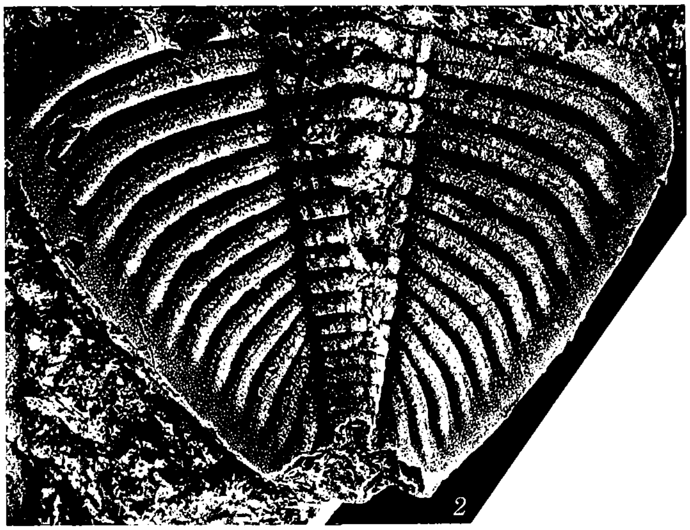
Figures 1a, b. *Odontochile syncrama,* new species. Two views of OU 8269. Cravatt Member, locality C1—P.

Figure 2. *Odontochile syncrama,* new species. Specimen with most of external surface preserved. OU 7198, ×2.3. Cravatt Member, locality P13.

Figure 3. *Odontochile litchfieldensis* Delo. Plaster cast of holotype, USNM 79089, ×2.6. Helderbergian, Litchfield, New York.

Figure 4. *Huntonia (Huntonia) lindenensis* (Delo). Cephalon with exoskeleton abraded but showing traces of micro-ornament. USNM79050, ×2.6. Linden Formation, Swayne's Mill, north of Camden, Tennessee.

Figure 5. *Huntonia (Huntonia) lindenensis* (Delo). Dorsal view of anterior cephalic process of large specimen. USNM 163977, ×2.3. Same horizon and locality.



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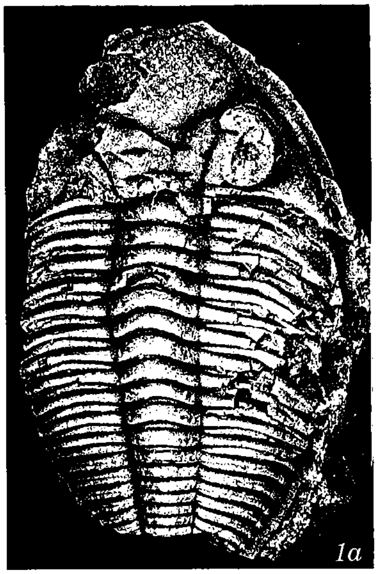

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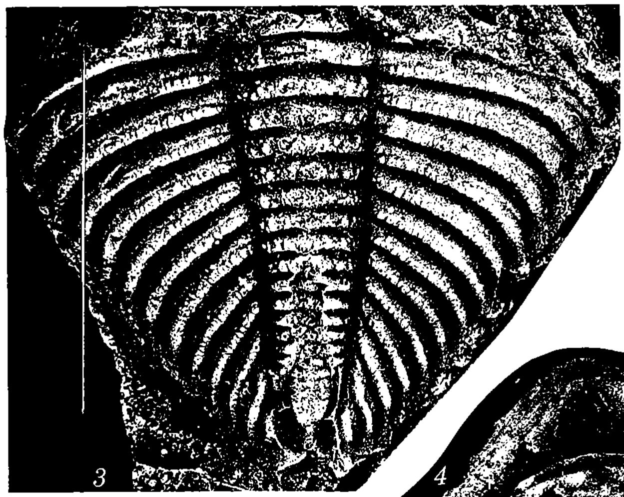

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Plate 30

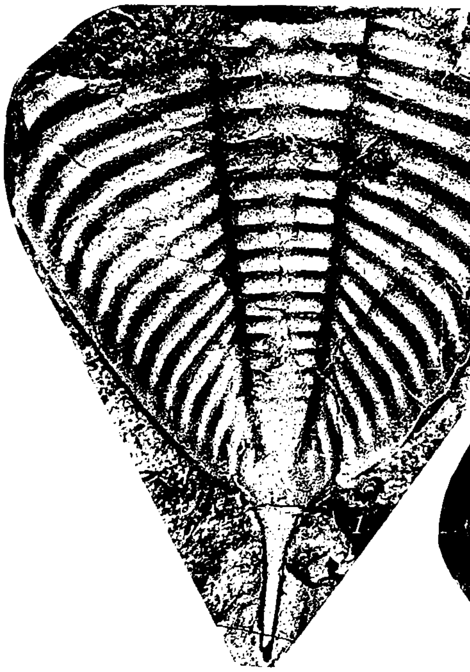
Figure 1. *Huntonia (Huntonia) acuminata* (Ulrich and Delo). Dorsal view of internal mold of pygidium, holotype. Helderbergian, Tishomingo County, Mississippi. USNM 99225, ×1.5.

Figures 2a, b. *Huntonia (Huntonia) purduei purduei* (Dunbar). Dorsal and ventral views of Type-B pygidium, USNM 143308, ×2. Ross Limestone, Pickwick Dam, Tennessee.

Figure 3. *Huntonia (Huntonia) purduei purduei* (Dunbar). Dorsal view of partly stripped Type-B pygidium, OU 7212, ×1.5. Haragan Formation, northeast of Bromide.

Figure 4. *"Odontochile" taffi* (Ulrich and Delo). Holotype pygidium. Note wide, flat doublure in right anterolateral corner. USNM 79037, ×2. Haragan Formation, Atoka quadrangle.

Figures 5a, b. *Phalangocephalus rutabulum,* new species. Dorsal and anterolateral views of latex cast of holotype cephalon. OU 6593, ×3. Bois d'Arc Creek.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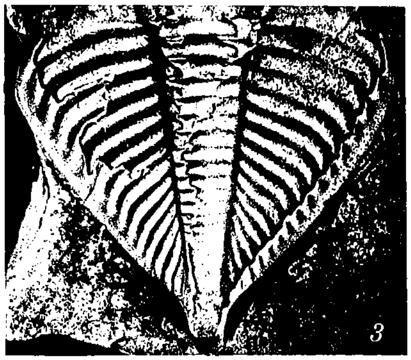
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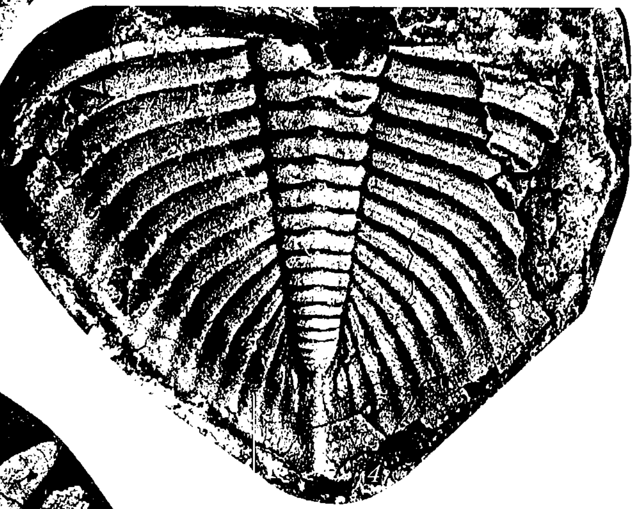
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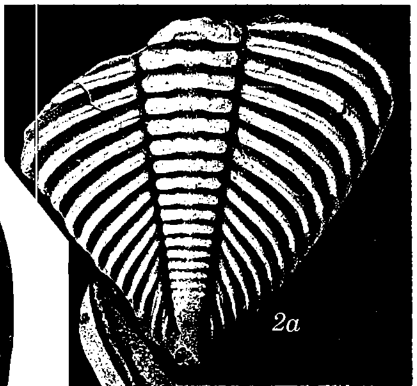

2a

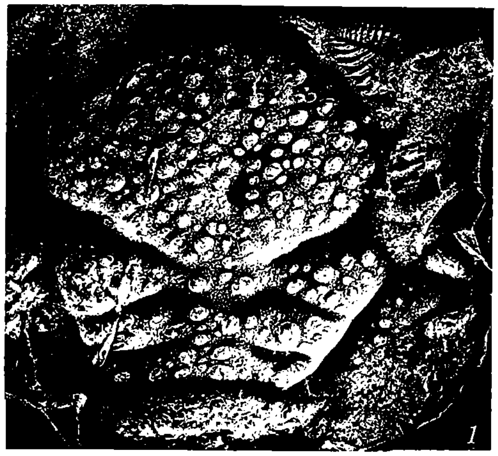

5b


2b

Plate 31

All specimens *Phalangocephalus dentatus* (Barrett), from Point Jervis Limestone, Trilobite Mountain, New York; housed in AMNH unless otherwise indicated.

Figure 1. Latex cast of part of cranidium to show details of ornament. ×2.
Figures 2a, b. Plaster cast of specimen from which most of exoskeleton has been stripped. ×1.5.
Figure 3. Same, originally figured by Hall and Clarke, 1888, plate 11A, figure 5. NYSM 4311, ×1.5.
Figure 4. Same, with marginal spines, almost complete. ×2.
Figure 5. Same, showing anterior part of cephalic doublure. Note particularly how doublure narrows and stands vertically lateral to hypostomal suture. ×2.5.
Figure 6. Part of genal region to show details of ornament. ×2.3.
Figure 7. Posterior end of pygidium in lateral view, showing ornament and almost complete terminal spine. ×2.
Figure 8. Plaster cast of internal mold of pygidium, originally figured by Hall and Clarke, 1888, plate 11A, figure 6. Dark spots on axis are air bubbles in cast. NYSM 4310, ×2.5.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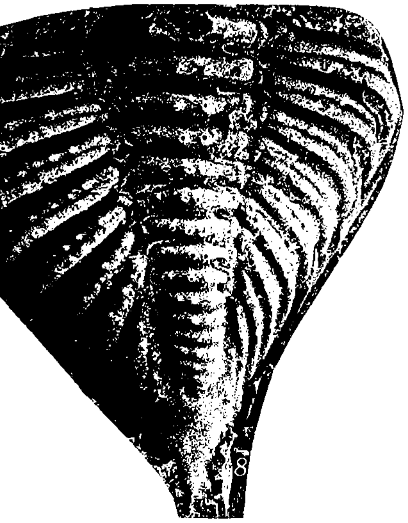
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Plate 32

All specimens *Leonaspis williamsi* Whittington, from Haragan Formation.

Figure 1. Almost complete specimen of Type B. See also plate 34, figure 4. OU 5276, ×4. White Mound.

Figures 2a, b. Almost complete specimen of Type B with cephalon tilted at high angle to thorax; right eye preserved. OU 6530A, ×4. White Mound.

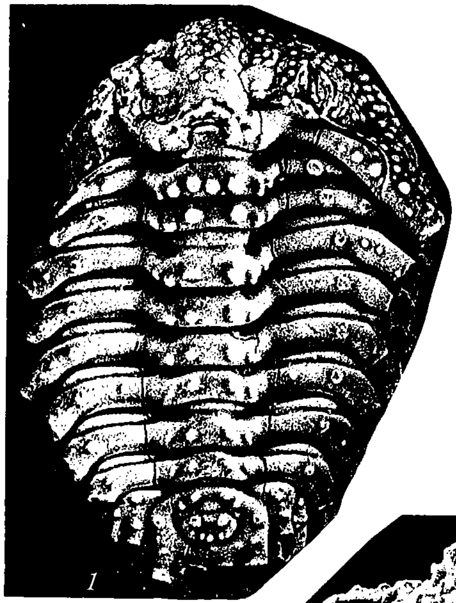
Figure 3. Small enrolled specimen of Type B viewed from front. Left eye is complete. OU 6530B, ×4. White Mound.

Figure 4. Specimen of Type B with well-preserved cephalic tubercles and marginal spines. ANU 21899, ×4. Old Hunton Townsite.

Figures 5a, b. Moderately large specimen of Type B with posterior thoracic pleural spines and marginal pygidial spines well preserved. OU 6531, ×5 and ×6. "Arbuckle Mountains."

Figure 6. Specimen figured by Whittington, 1956, plate 58, figure 2. USNM Collection, ×3.

Figures 7a, b. Dorsal and ventral views of isolated pygidium. ANU 21892, ×7. Old Hunton Townsite.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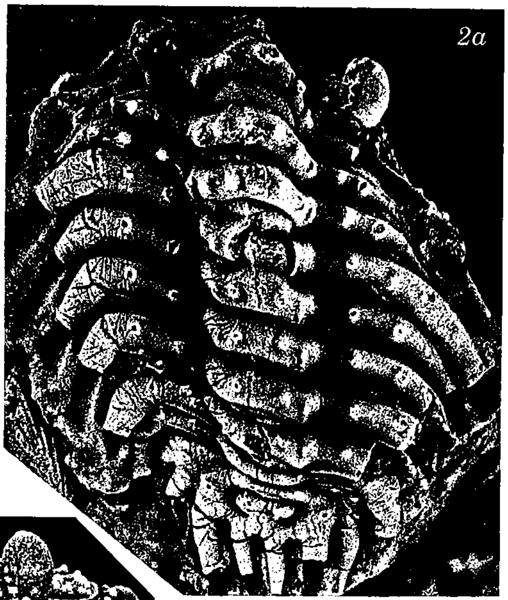
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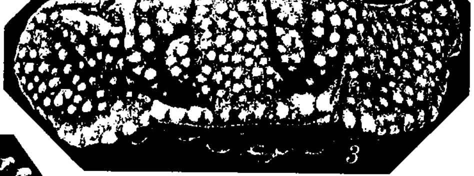
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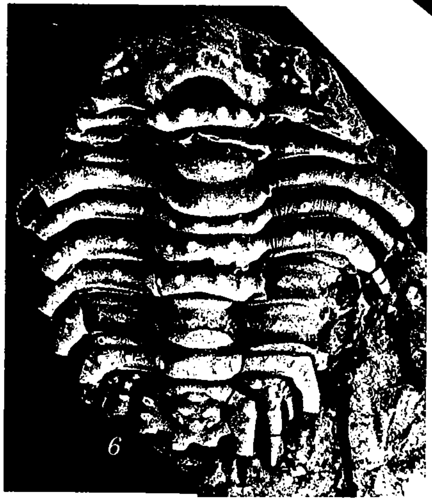
7a


7b


5a


5b


6


2b

Plate 33

All specimens are *Leonaspis williamsi* Whittington, from Haragan Formation.

Figures 1a-c. Three views of free cheek of Type A. ANU 21892A, ×4. Old Hunton Townsite.

Figure 2. Specimen of Type A showing what is thought to be natural curvature of thoracic and pygidial spines. ANU 14848, ×3. Old Hunton Townsite.

Figures 3, 9. Specimen of Type A (figured by Whittington, 1956, pl. 58, fig. 1), showing aberrant single spine on pygidial margin in mid-line. USNM Collection, ×3 and ×6. Vines dome.

Figure 4. Posterodorsal view of specimen of Type A (figured by Whittington, 1956, pl. 57, figs. 12-14). USNM Collection. White Mound.

Figure 5. Dorsal view of specimen of Type A showing unusually well-preserved pleural spines. OU 5273, ×5. Old Hunton Townsite.

Figure 6. Partly disarticulated specimen of Type A. Note anterior pleural spines on several segments. ANU 21903, ×5. Old Hunton Townsite.

Figure 7. Type-A specimen with pygidium and axis of thorax well preserved. ANU 21895, ×5. Old Hunton Townsite.

Figure 8. Intermediate type with well-developed tuberculation along posterior pleural spines. OU 6532, ×5. White Mound.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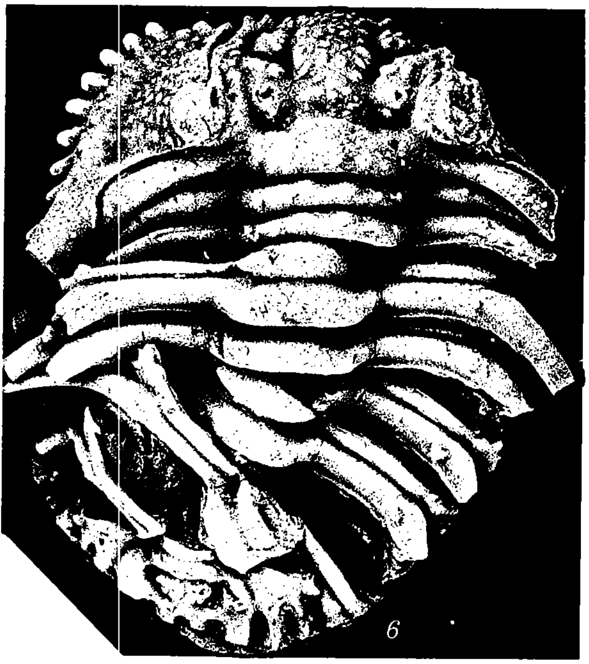
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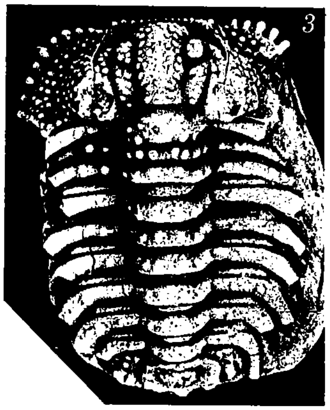
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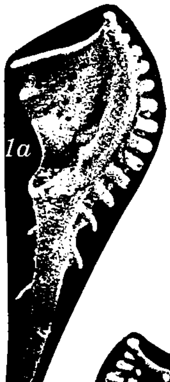
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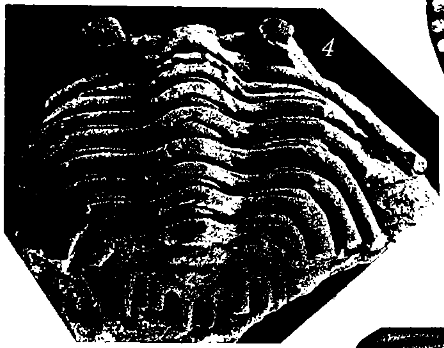
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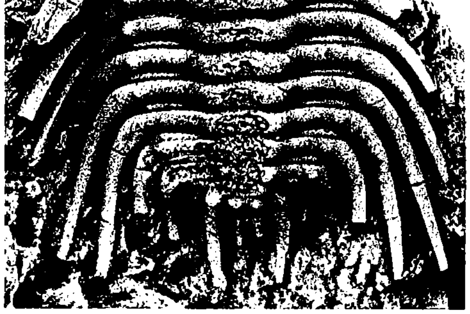
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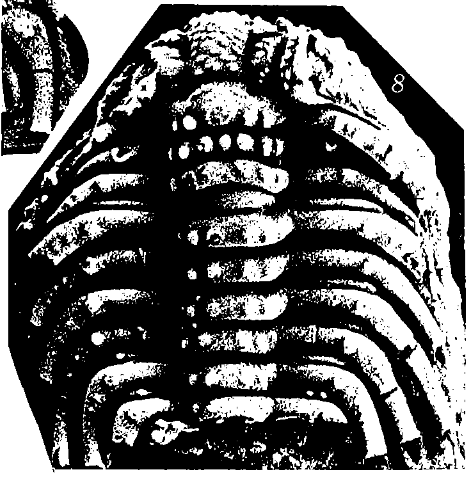
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Plate 34

Figures 1, 2. *Leonaspis tuberculata* (Hall). Isolated thoracic segment and free cheek. YPM 3586C, ×4. Clarksville, New York.

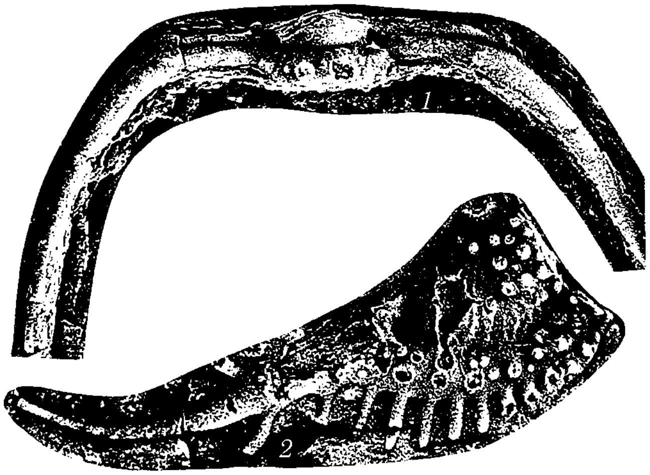
Figures 3a, b. *Leonaspis williamsi* Whittington. Ventral and dorsal views of free cheek probably of Type B. ANU 21892, ×5. Haragan Formation.

Figure 4. *Leonaspis williamsi* Whittington. Lateral view of specimen of Type B to show shapes of anterior pleural spines of thorax. Specimen has been prepared by airbrasion; thus most of spines are slightly worn. That on fifth segment has its posterior part broken. OU 5276, ×5. Haragan Formation, White Mound.

Figures 5a-d. *Leonaspis williamsi* Whittington. Anterior, posterior, ventral, and dorsal views of hypostome. USNM 173903; a, b, ×5; *c, d,* ×11. Haragan Formation, Old Hunton Townsite.

Figure 6. *Leonaspis tuberculata* (Hall). Isolated hypostome. YPM 3580C, ×16. Clarksville, New York.

Figures 7a-d. *Dicranurus hamatus elegantus,* new subspecies. Posterior, ventral, dorsal, and oblique lateral views of hypostome. OU 5283; *a-c,* ×7; *d,* ×10. White Mound.



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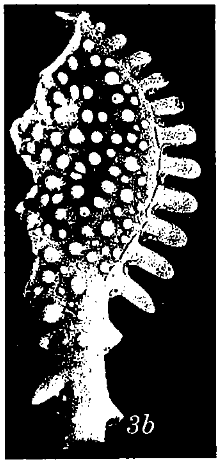
2

3a



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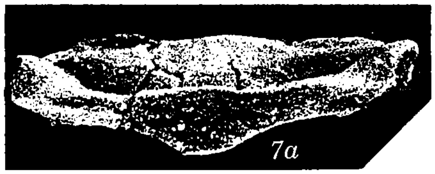

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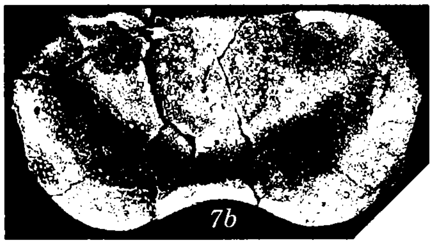
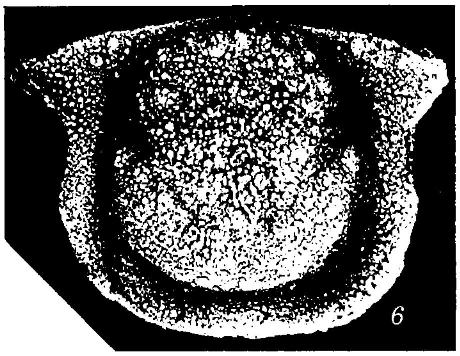


7b

5a

5b

7d



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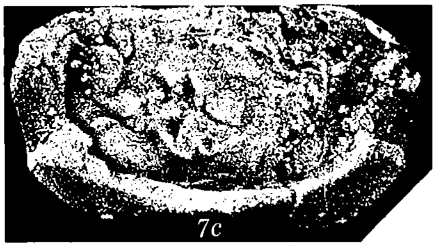

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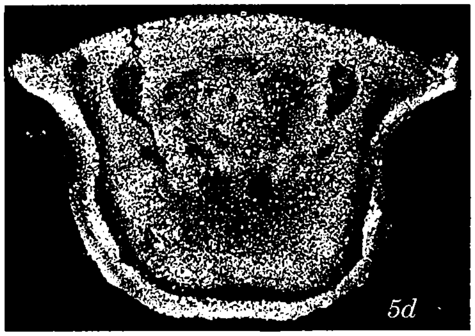

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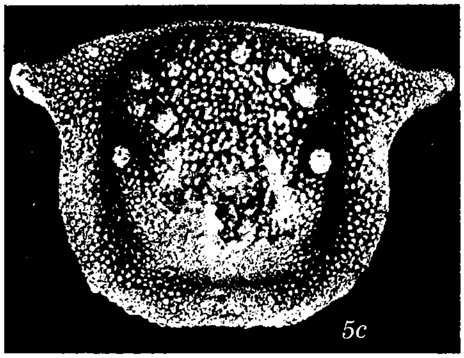


5c

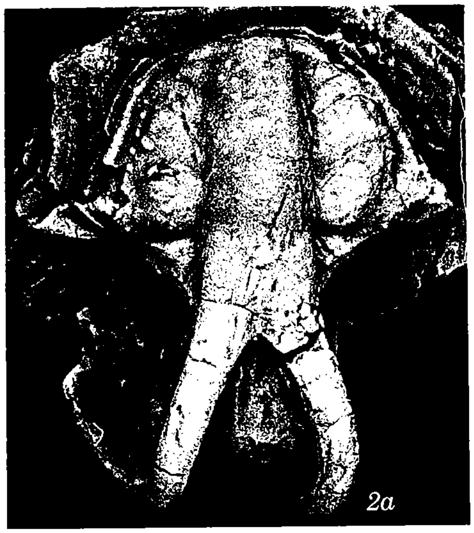
Plate 35

Figure 1. *Dicranurus hamatus* (Hall). Specimen from Clarksville, New York, with exoskeleton present on most of occipital ring and spines. YPM 6567, ×2.1.

Figures 2a, b. *Dicranurus hamatus elegantus,* new subspecies. Dorsal and anterior views of cranidium. OU 6339, ×2. Haragan Formation, Old Hunton Townsite.

Figures 3a-c. *Dicranurus hamatus elegantus,* new subspecies. Oblique, dorsal, and anterior views of holotype. Anterior pleural spines on thorax are complete. Note shape of rostral plate as shown on right side of *3c*. OU 5275; *a, b,* ×1.7; *c,* ×3.3. Haragan Formation, Old Hunton Townsite.


1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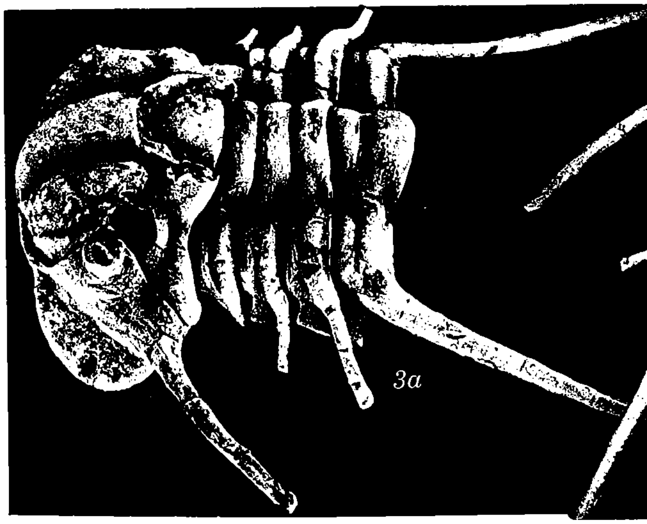
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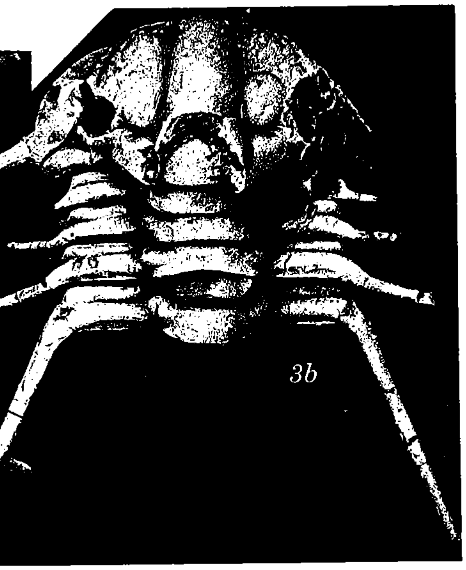
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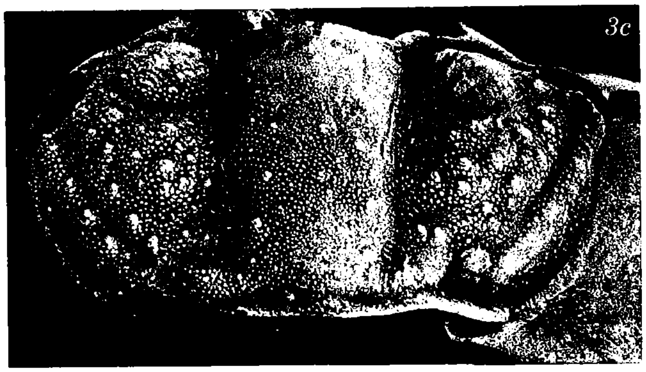

3c


2b

Plate 36

All specimens *Dicranurus hamatus elegantus,* new subspecies, from Haragan Formation.

Figure 1. Specimen with well-preserved pygidium and posterior thoracic pleural spines. OU 3429, ×2.4. Old Hunton Townsite.

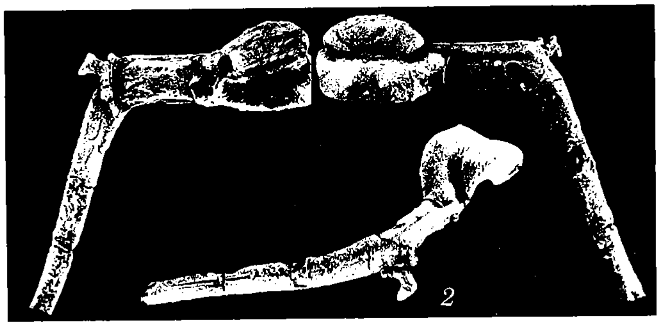
Figure 2. Isolated fourth thoracic segment taken from specimen in figure 5 of this plate; ventral, dorsal, and oblique lateral views. OU 6540, ×2. Old Hunton Townsite.

Figures 3a, b. Holotype; anterior view and ventral view of free cheek; genal spine incomplete. Note wide doublure and shape of connective suture. OU 5275, ×2.2. and ×2. Old Hunton Townsite.

Figures 4a-c. Lateral and two dorsal views of thorax. Anterior pleural spines of thorax are almost complete. Note greatly reduced posterior and anterior pleural spines on second last segment shown. OU 5282, ×2, ×2.1, and ×7.

Figures 5a-c. Oblique posterior, posteroventral, and dorsal views of small incomplete cranidium. Note high complete palpebral lobe and complete posterior occipital band. OU 6540, ×2, ×3, and ×3.

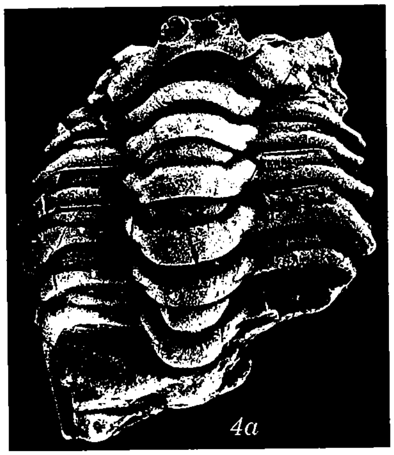
1



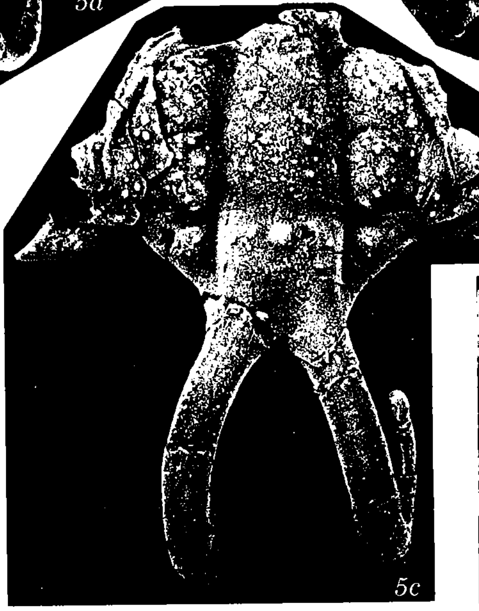
2

5a

3b



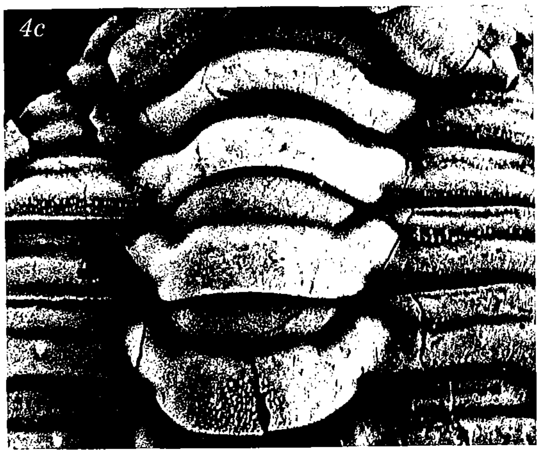
4a



5c

5b

4b



4c

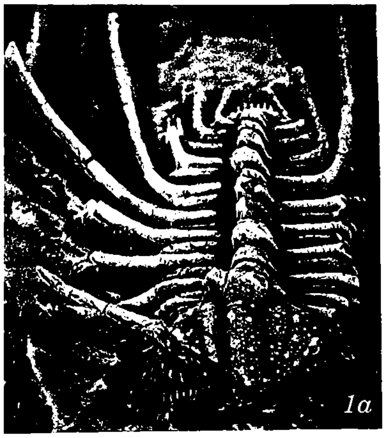
3a

Plate 37

All specimens *Ceratonurus* sp., from Haragan Formation.

Figures 1a-f. Various views of USNM 134731. In *1b,* anterior pleural spine on 5th segment has its tip separated from main body, but 6th spine is complete. *a, d, e, f,* ×2; *b,* ×6; *c,* ×4. White Mound.

Figures 2a-d. Various views of incomplete pygidium and last five thoracic segments. In *2d,* tips of anterior pleural spines have been broken. Note presence of 3d small spine on last and 3d last thoracic segments. ANU 21900, ×3, ×6, ×3, and ×5. Old Hunton Townsite.

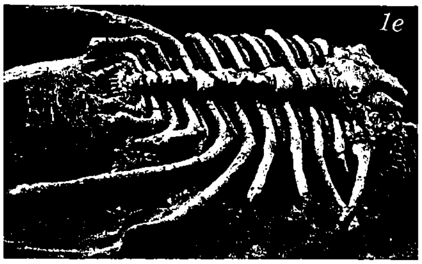


1a

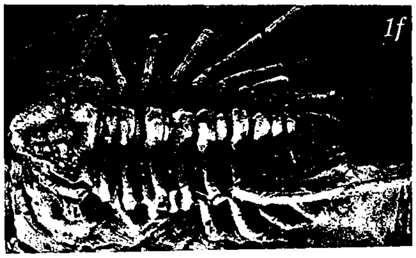
1b

1c

1d



1e



1f

2a

2b

2c

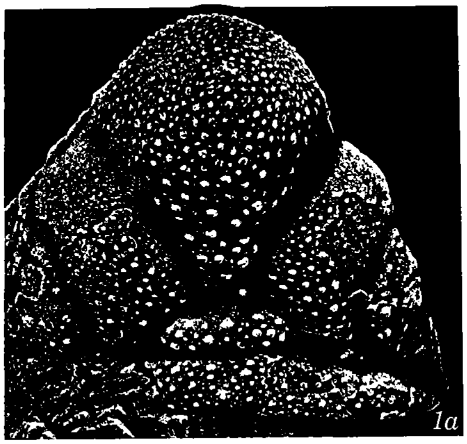
2d

Plate 38

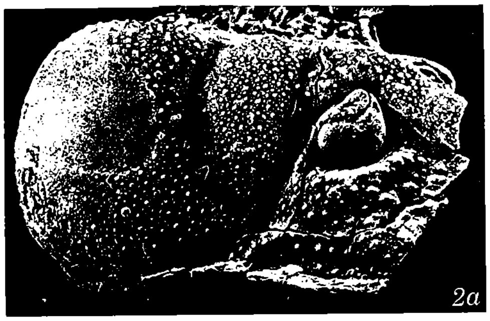
Figures 1a, b. *Echinolichas*? *coccymelum,* new species. Dorsal and oblique views of cranidium of Type A with most of exoskeleton preserved. OU 6535A, ×1.4. Haragan Formation, Old Hunton Townsite.

Figures 2a-c. *Echinolichas*? *coccymelum,* new species. Oblique, partial dorsal, and anterior views of Type-A holotype. OU 4962, ×1.5. Haragan Formation, Old Hunton Townsite.

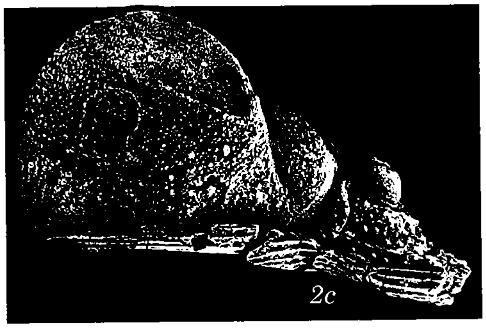
Figures 3a-c. *Echinolichas*? *coccymelum,* new species. Oblique, posterior, and dorsal views of best preserved cranidium of Type B. OU 3446, ×1.4. Haragan Formation, northeast of Bromide, Coal County.


1a


1b


2a


2b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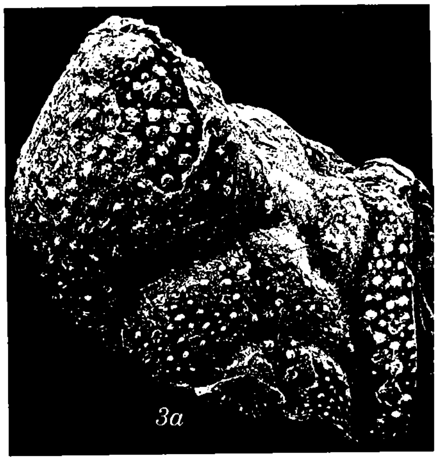
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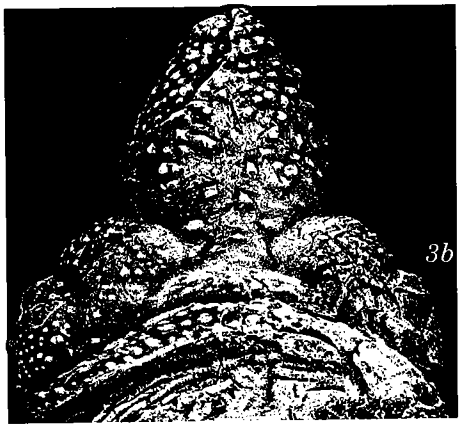

3b


3c

Plate 39

Figures 1a, b. *Echinolichas? coccymelum,* new species. Dorsal and oblique views of internal mold of small cranidium. OU 6534, ×1.5. Haragan Formation, locality C1.

Figures 2a, b. *Echinolichas? bigsbyi* (Hall). Oblique and dorsal views of latex replica of internal mold from Hall collection. AMNH 2610/1, ×1.5. Helderbergs.

Figures 3a, b. *Echinolichas? coccymelum,* new species. *3a,* ventral view of holotype, an imperfect cephalon, showing hypostome, right side of rostral plate, connective suture, and doublure. *3b,* latex cast of hypostomal surface showing details of ornament. OU 4962, ×1.5 and ×2.2. Haragan Formation, Old Hunton Townsite.

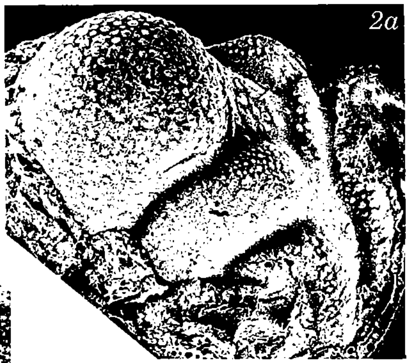
Figure 4. Same. Anterior view showing shape of connective suture, ×3.

Figure 5. *Echinolichas? coccymelum,* new species. Incomplete and partly stripped pygidium, also showing part of doublure. OU 6535B, ×1. Haragan Formation, locality C1.

Figure 6. *Echinolichas? bigsbyi* (Hall). Plaster cast of left side of pygidium with marginal spines broken. Specimen figured by Hall, 1861, plate 77, figure 8, now labelled AMNH 2610/2; ×1.5. Helderbergs.

Figures 7, 8. *Echinolichas? bigsbyi* (Hall). Plaster casts of two hypostomes from Hall collection. Figure 8 previously figured by Hall, 1861, plate 77, figure 7. Specimens now labelled AMNH 2610/3; ×1.5 and ×1.8.


1a


2a


2b

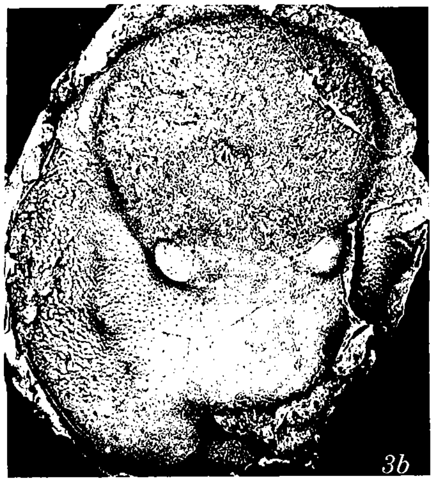

1b


7


8


6


4


3b


3a


5

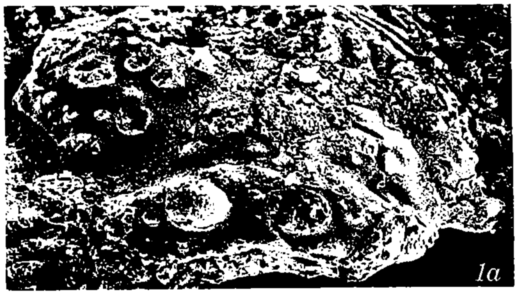
Plate 40

Figures 1a, b. ?*Terataspis* sp. Posterodorsal and dorsal views of fragment of occiput. OU 7192, ×1.5. Frisco Formation, locality S1—B.

Figures 2a, b. *Echinolichas? coccymelum,* new species. Two fragmentary pygidia. OU 6533, ×1.5, and OU 6536, ×1.5. Haragan Formation, Old Hunton Townsite and near locality P1, respectively.

Figures 3a, b. *Echinolichas? coccymelum,* new species. Part of doublure and corresponding dorsal surface of pygidial fragment preserved beneath holotype. Note that margin of fragment seems to be complete, and no spines are present. OU 4962, ×1.5 and ×2.3. Haragan Formation, Old Hunton Townsite.

Figures 4a-d. *Huntonia (Huntonia) oklahomae* (Richardson). *a-c,* anterior, ventral, and dorsal views of incomplete cephalon with most of ornament stripped from glabella, and encrusting polyzoan on anterior lobe. *d,* enlargement of anterior process. OU 3410, ×2, ×1.6, ×1.6, and ×2.5. Haragan Formation, Old Hunton Townsite.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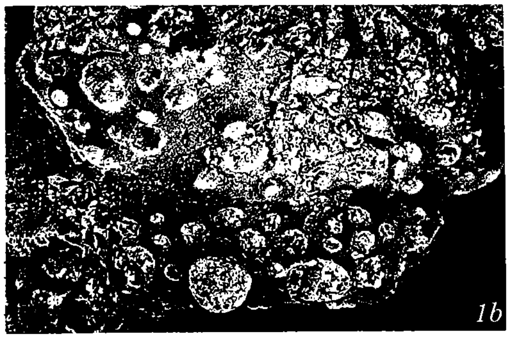
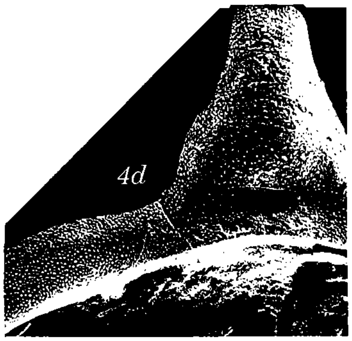

1b


2a


2b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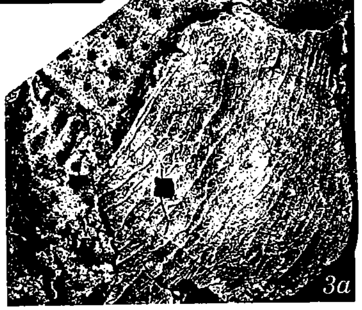
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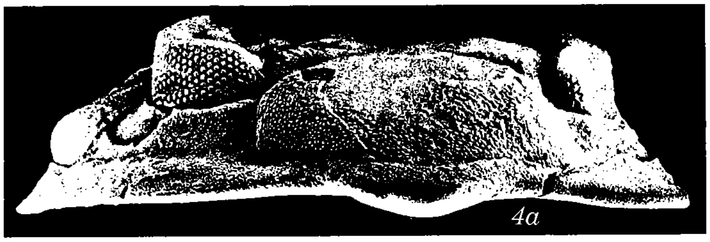
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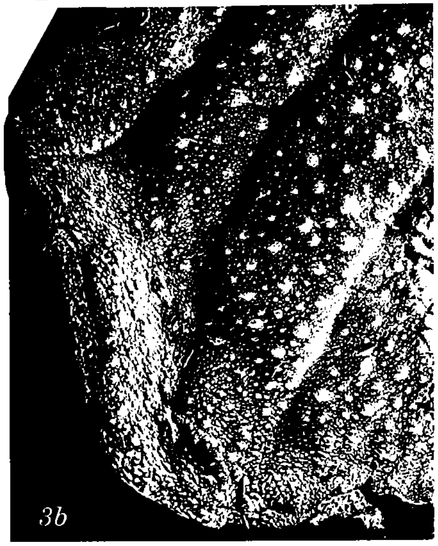
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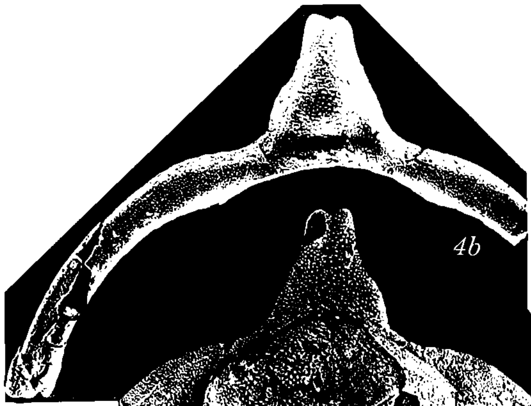
4b


4c

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