68-15, 206

HU, Chung-Hung, 1924-
ONTOGENY AND SEXUAL DIMORPHISM
OF LOWER PALEOZOIC TRILOBITA.

University of Cincinnati, Ph. D., 1968
Geology

University Microfilms, Inc., Ann Arbor, Michigan

ONTOGENY AND SEXUAL DIMORPHISM OF LOWER PALEOZOIC TRILOBITA

A dissertation submitted to
The Graduate School
of the University of Cincinnati
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy
1968

by
Chung-Eung Hu
A.B. Northeastern University, Mukden, China, 1947
M.S. University of Tokyo, Tokyo, Japan, 1957

UNIVERSITY OF CINCINNATI

May 29 19 68

I hereby recommend that the thesis prepared under my supervision by Chung-Hung Hu

entitled Ontogeny and Sexual Dimorphism of Lower Paleozoic Trilobita

be accepted as fulfilling this part of the requirements for the degree of Doctor of Philosophy

Approved by:

Kenneth E. Caster

William A. Oswald

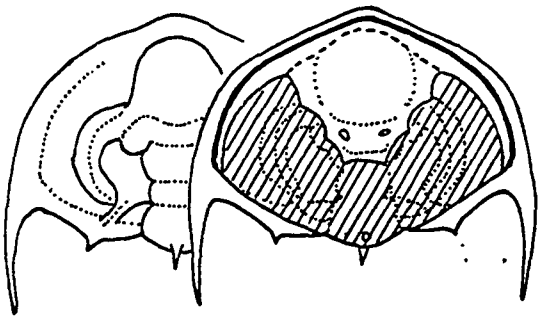
William F. Jenkins

Form 668—Grad. Sch.—1M—7-63

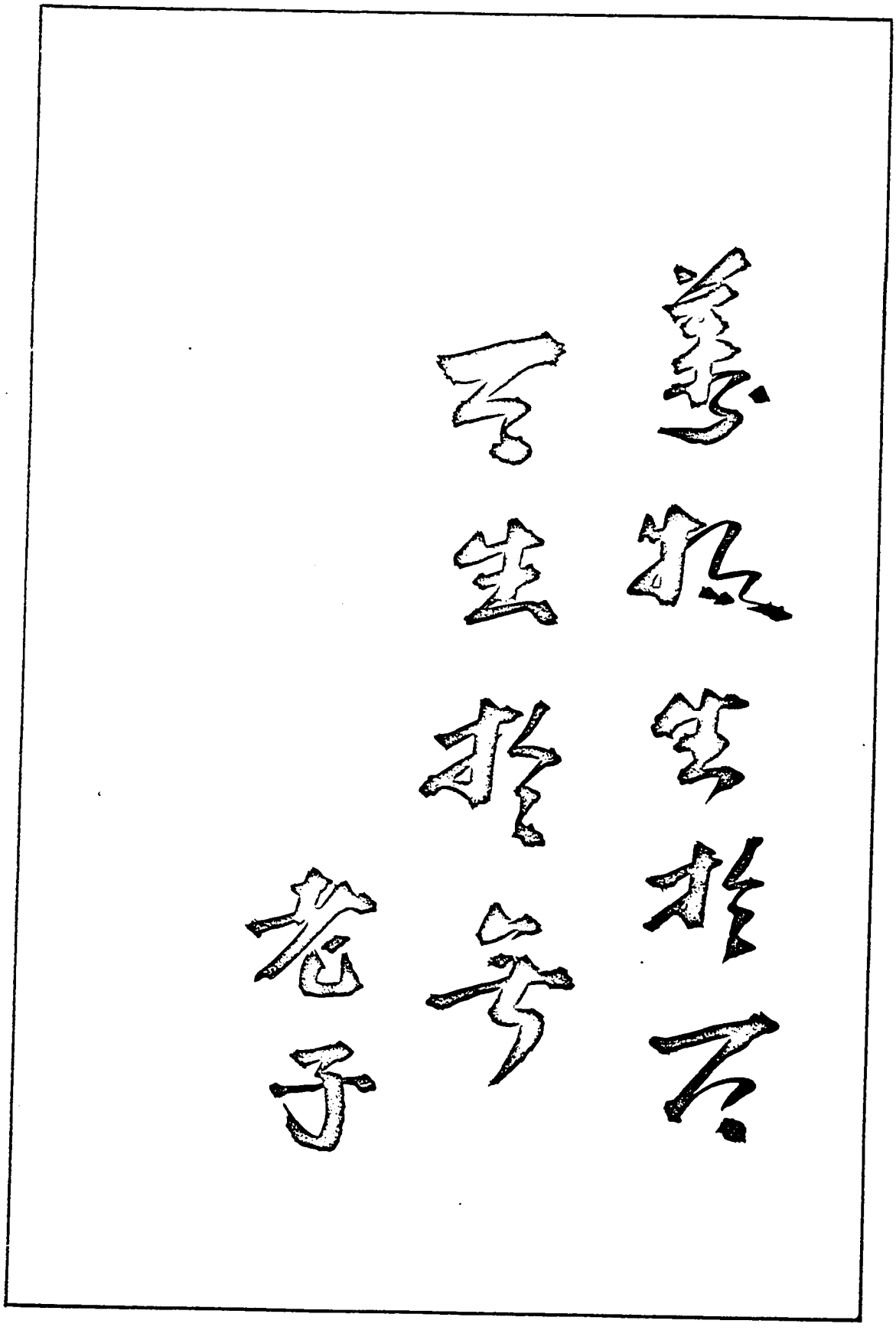
二葉實學

胡忠恒著

凌河



一九六八荷月



Organisms derive from organisms;
Life from the lifeless.

Lao-Tze, 604-531 B.C.

ABSTRACT

In the present research twenty-six genera and species of Lower Paleozoic trilobites are described. These include four new genera and seven new species. Among these, twenty-three species show an excellent sequence of ontogenetic stages, and twelve species show distinct bimodalism of adults which is thought to be attributable to sexual dimorphism. The life cycle of trilobites is divisible into three periods: the protaspid, meraspid, and holaspid periods. The protaspid period is subdivided sequentially into anaprotaspid, metasprotaspid, and paraprotaspid stages, based primarily on the number of axial rings and the presence or absence of the protopygidium. The meraspid period is likewise subdivided into early and late meraspid stages, based mainly on the presence or absence of the anterior cephalic brim, position of the palpebral lobes, and facial sutures. The holaspid period shows ephebic characters which are those customarily employed for specific diagnosis and are essentially unaltered throughout the remainder of the life span. The presumed adult sexual differences comprise variation in body size, nature of the prosopon ("ornament"), and bimodal ratio. The "females" have a statistically larger body, without distinct prosopon, and are less numerous than the "male" forms. The relative abundance of the two forms is the "sexual ratio". The ontogenetic development of the polychaete worms, crustaceans, and xiphosurans is compared with that of trilobites. Both trilobite and crustacean larvae possess two primary somites and five cephalic segments, whereas

the xiphosuran larva has four primary somites and six or seven cephalic segments. If these criteria are of phylogenetic significance, it would seem that Trilobita and Crustacea may be more closely related to one another than are trilobites to merostomes. The undifferentiated serial appendages of trilobites are quite similar to those of polychaetes, whence they may well be derived, and probably can serve as a paradigm of the primitive limb structure within the Arthropoda. The variously diversified appendages of crustaceans and xiphosurans are functional, and all are quite possibly derived from serially uniform appendages such as those of trilobites. Simplification, complication, and differentiation have been evolutionarily operative in the divers arthropod groups. Examination of the larval development of the polychaete, Pisione remota, shows many similarities to that of earliest trilobites, especially Laudonia and Olenelloides of the Lower Cambrian. In both these annelids and the trilobites the cephalization is accomplished by a forward migration of the body segments and elongation of the eye rings. These ontogenetic similarities, together with the generalized nature of trilobite appendages, seem strongly to support the hypothesis of "polychaete origin of the trilobites".

The degree of separation of the librigenae and rostrum of trilobites appears to have great phylogenetic and classificatory significance. Four groups can be differentiated on this basis: Monorostraloid, Trirostraloid, Birostraloid, and Holorostraloid. These relations may eventually serve as major taxobases. The agnostids are viewed as representing an Architrilobitoid group, and

as deserving a taxonomic rank equal to Trilobita. Both ontogenetic and morphologic characters of the architrilobites are quite different from those of the rest of the trilobites. The architrilobite larvae possess the same number of primary somites as typical trilobites, but the adult has four (instead of five) cephalic segments. The similarity of the architrilobite cephalic and pygidial shields in size and shape, and the presence of only two or three thoracic segments further sets them apart.

ONTOGENY AND SEXUAL DIMORPHISM OF LOWER PALEOZOIC TRILOBITA

by

Chung-Hung Hu

Text-figures

Plates

INTRODUCTION

There has been great progress in the ontogenetic study of trilobites during recent years. This has been especially due to the discovery of silicified materials which have not only the dorsal morphologic characters well preserved, but also the marginal spines and certain ventral structures, including the hypostoma and rostrum. These fine specimens give new insight into the larval mode of life and afford new data of taxonomic importance. The most notable studies of this new material have been done by Whittington and Evitt (1954, 1959a), working on Middle Ordovician trilobites of Virginia; by Palmer (1957, 1962) and Robison (1964), studying the Lower to Upper Cambrian trilobites of Nevada and Utah; and by Ross (1951) and Hintze (1952), studying the Lower Ordovician trilobites of Nevada and Utah.

Because of the extraordinary perfection of the silicified larval remains and the recentness of their discovery and study, and especially the ease with which this material can be recovered by acid treatment, other types of larval documentation have tended to be neglected or discounted. Non-silicious remains require far more time and pains for extraction and preparation, yet for many places and horizons, these are the only larval evidence available. Moreover, as the photographas here presented show, the calcareous remains may rival the siliceous if properly pursued with microscope and fine dissecting needle.

The materials here studied include both calcareous and silicified specimens representing twenty-three species, ranging in age from Lower Cambrian through Upper Ordovician and showing continuous ontogenetic sequences. Except for two genera from the Scandinavian Peninsula, the materials were mostly collected from North America: from Mexico to the Canadian Rockies and from New Brunswick to Utah (Index Map, opp. p. 7).

Statistical studies of adult specimens commonly show that a given species of trilobite possesses bimodally distributed characters, a phenomenon here attributed to sexual dimorphism. It is the assumption here that the most abundantly represented specimens were males, either having relatively small bodies without special prosopon, or large bodies with strongly modifying prosopon. The less numerous female are large-bodied without special prosopon or small-bodied with slightly modifying prosopon. These morphologic and sexual ratio differences seem to correlate with sexual dimorphism in Recent Arthropoda, such as Insecta, Crustacea, and Merostomata. Twelve species are described which show these bimodal traits. By extension, this phenomenon is to be expected as a general trait of trilobites. Its recognition may well materially reduce the number of "species" now current in trilobite literature.

The ontogenetic development of a complete growth sequence is divided into three periods: the protaspid, meraspid, and holaspid. The protaspid period is subdivided into anaprotaspid, metaprotaspid, and paraprotaspid stages; the meraspid period into early and late meraspid stages; and the holaspid period lacks subdivisions.

In the earliest ontogenetic developmental instars, or

protaspid stage of the trilobite larva, the shield contains two primary somites with a procephalon and a generative pygidium. It does not resemble the "trilobite" stage of the ontogenetic development of Xiphosura ("Limulus") but rather the nauplius of crustaceans, since the Xiphosura larvae have four primary somites whereas both trilobites and crustaceans possess only two. In adults, the cephalon of both crustaceans and trilobites have antennules and four post-oral segments, whereas the xiphosuran lacks antennules and contains more than six post-oral segments. The ontogenetic development and cephalic structure suggest that the phylogenetic relationship between trilobites and crustaceans is closer than that of trilobites to merastomes. The trilobite is a true protarthropod with many morphologic and ontogenetic features similar to those of polychaetes. The morphologic feature of the polychaete, Pisione, is very similar to that of olenellids and is highly suggestive of the possibility that the Trilobita may be directly evolved from Pisione-like polychaetes by secretion of an external skeleton, forward migration of body segments to form a cephalon, and elongation of the eye rings.

The variously differentiated appendages of arthropods, i.e., uniramous, biramous or triramous appendages, are best interpreted as independent functional adaptation of trilobitiform appendages. Simplification, complication, and differentiation have operated in various derivative evolution. Thus, the uniramous appendages, like those of trilobites or geologically older crustaceans, are original and the biramous (bifurcate) or triramous appendages are derived. If the notopodium of polychaetes is homologous with the pleural spine or

tergal spines of trilobites, limuluids, and crustaceans, the neuropodium and parapodial setae should be equivalent to the uniramous or endopodite appendage and gill branch of the epipodite (Fig. 32). Therefore, the exopodite of crustaceans would appear to be a subsequent development. The structure and the uniform serial arrangement of trilobite appendages show the same basic plan as those of polychaetes.

The basis for a fundamental classification of Trilobita is by no means yet known. A good case can be made for excluding the agnostids as Architrilobitoids from the Trilobita, ss. The present study has brought out the potential importance of the Librigeno-rostrum organization as a major taxobasis for the Trilobita, ss. Thus, four groups are here distinguished: In the monorostraloid group the complete rostrum is the perrostrum; this is the condition in olenellids; in the trirostraloid group the librigeno-rostrum is separated into three parts; this condition is represented by Redlichia and most of ptychopariids; in the birostraloid group the librigeno-rostrum is separated into two parts, as in asaphids, Bathynotus, and Remopleurides, etc.; and the holorostraloid group lacks separation but differs from the monorostraloids by the dorsal or super-marginal suture; examples are the trinucleids, phacopids, dalmanitids, etc. The Architrilobitoids are not strictly comparable with typical trilobites, since their cephalon comprises four segments only: a procephalon and three post-oral segments. They may not even represent a trilobite taxon due both to the ontogenetic and morphologic differences. The agnostids, eodiscids, etc. represent this group. They may equate in taxonomic rank with Trilobita.

The terminology of the present study for the most part follows the

Treatise on Invertebrate Paleontology, (Part O, Arthropoda 1). The figured and type specimens are mainly stored in the Geological Museum, University of Cincinnati, Cincinnati, Ohio (U.C.M.), and partly in the United States National Museum (U.S.N.M.).

ACKNOWLEDGEMENTS

The writer wishes to express his gratitude to the many people who have contributed to the successful completion of this work. Special thanks go to Dr. Kenneth E. Caster under whose direction this work was prepared. He gave generously of his time and was a constant source of inspiration. Thanks are also due Dr. R. Endo, Professor of Geology, Saitama University, Japan and Dr. T. Kobayashi, Professor of Geology, University of Tokyo, Japan for their long-term encouragement.

I am grateful to Drs. H. B. Whittington, Harvard University, and B. F. Howell, Princeton University for their criticism and helpful suggestions. Dr. A. R. Palmer, United States Geological Survey, permitted me to describe his Wah Wah Range collection including Dunderbergia ? anyta and Dytremacephalus granulosus; Dr. F. Rasetti, formerly of Johns Hopkins University, permitted me to describe his Virginia collection of Libertella corona and Phaseolops conus; and Dr. Ch. Lochman-Balk, New Mexico Institute of Mining and Technology, permitted me to describe her Mexico and Missouri collections, including Olenellus truemani and Kormagnostus simplex. Dr. J. L. Wilson, Rice University, generously permitted me to describe his British Columbia collection, including Laudonia canadiensis. For their valuable discussion of the identifications, I also extend my warm thanks to these specialists. Many thanks go also to my Paleontology classmates at the

University of Cincinnati for their contributions during a three year (1963-1966) seminar course on the Arthropoda, through which I have profited by much information related to the present studies.

The writer is deeply indebted to Dr. C. G. Bookhout, Director of Duke University Marine Laboratory, Beaufort, North Carolina, for his many suggestions on the ontogenetic development of modern crustaceans and under whose supervision the writer has had the rare opportunity to study the ontogenetic development of polychaetes in comparison with that of trilobites.

Finally, I must express my heartfelt thanks to my very good friend, Mr. Michael Stephens, formerly of the Geology Department, University of Cincinnati (now at California Institute of Technology) for assistance with the English text and discussion of certain problems involved in the present study. To Mrs. Wanda Osborne, Secretary of the Geology Department, University of Cincinnati, who typed the manuscript, I also wish to express deep thanks. The financial expenses of the present work were mainly supported by the Museum Fellowship and the Nevin M. Fenneman Fund of the University of Cincinnati, and partly by the National Science Foundation during two summers of study (1966-1967) at the Duke University Marine Laboratory at Beaufort, North Carolina.

Index map of the geographic distribution of the described materials

Loc. 1. North of Radium, west of the Columbia River, British Columbia, Canada; 2. West side of South Boulder Creek, W. Madison County, Montana; 3. Sheep Mtns., Sundance, E. Wyoming; 4. Lead, Deadwood, South Dakota; 5. North of Mink Creek, Preston quadrangle, Idaho; 6. Princeton, Wasatch Mtns., Utah; 7. Santaquin Canyon, NE side of road, Wasatch Mtns., Utah; 8. Wah Wah Range, Utah; 9. Caborca, northwestern Sonora, Mexico; 10. St. Francois County, South Bonneterre, Missouri; 11. Cincinnati, Ohio; 12. Park Hills, W. Covington, Kentucky; 13. Willow Grove, 3 miles southwest of Woodstock, Virginia; 14. Kennebec River, St. John, New Brunswick, Canada; 15. Ringsaker Station, north of Oslo, Norway; 16. Nye, southeast of Joukoping, Sweden.

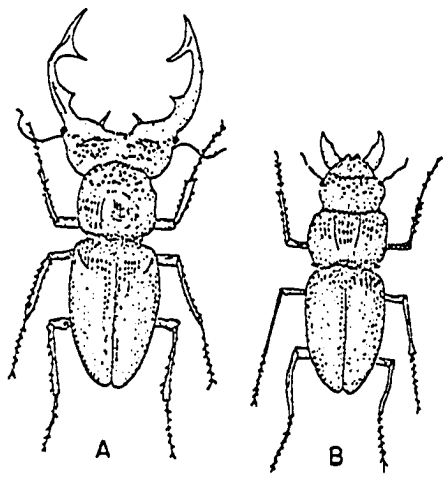
Index map of the geographic distribution of the described materials.

I. SEXUAL DIMORPHISM

Statistical study of specimens of the same species of trilobite often shows several variable minor features: the shape, length and width of the glabella, width of the librigenae and hypostoma, length of the occipital spine, the number of axial rings on the pygidium, the shape of the terminal portion, the width of the marginal border, and the convexity of the skeleton. Moreover, these variables are essentially bimodal in corresponding parts. These variable characteristics have been interpreted by many students as being largely the effects of preservation, or in some instances as specific differences. However, these features are constant and bimodal in undeformed specimens representing many genera and species. Dimorphism seems to be a common feature of trilobites, as it is in many arthropods. This trilobite dimorphism is believed to be sexual and the criteria for ascertaining the sexual identity of dimorphic forms now seem to be at hand.

1. Morphologic Criteria

Very frequently the male differs from the female in other respects than the nature of the reproductive organs, i.e., in size, prosopon, and the like; when such differences are strongly marked the species is said to be sexual dimorphic. This phenomenon is especially recognized in living organisms. The differentiation of species into two distinct sexual forms is universally found in all higher animals as well as in many plants and lower animals. In modern animals, especially in



Text-fig. 1: Sexual dimorphism of the stag-beetle Lucanus.
A. male form; B. female form.

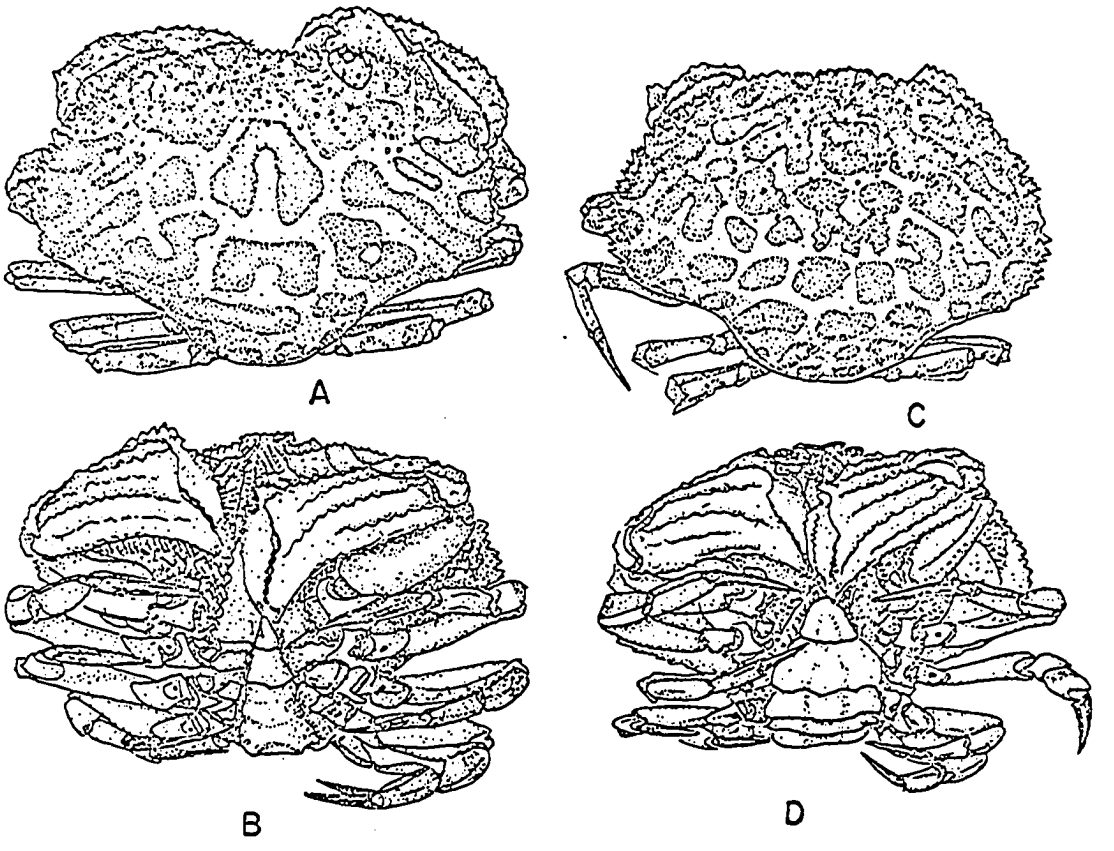
(Redrawn from Hanson, 1964.)

arthropods, the spinosly armored, large individuals of a species are commonly male, while those without armour or slender and smaller sized are the female. In West Indian Hercules beetle (Dynastes hercules), the male has a larger body and two large horns on the middle of the head, whereas the female has a small body and a hornless head. In the stag-beetles (Lucanus) (text-fig. 1), the male is larger and has two hypertrophis mandibles, whereas the female has shorter specialized mandibles. In the boreal primitive-weevel (Eupsalis minuta), the male is larger than the female and has a pair of powerful mandibles, the female has considerably smaller mandibles, which are prolonged into a slender snout. In the rhinoceros-beetle (Dynastes tityrus), the male bears three horns, one larger and two smaller on the middle of the head, and is larger than the female, which has only a small tubercle on the head.

Text-fig. 1. Sexual dimorphism of the stag-beetle Lucanus.
A. male form; B. female form. (Redrawn from Hanson, 1964.)

In Hepatus ephelitus, a common decapod crab, (collected in Channels a few fathoms in depth at Beaufort, North Carolina) the female is smaller than the male, and possesses a broad abdomen and shorter chelipeds (text-fig. 2).

Text-fig. 2: Hepatus ephelitus (Linnaeus). A, B, dorsal and ventral views of male form; C, D, dorsal and ventral views of female form. Notice the different sized abdomens.



Text-fig. 2: Hepatus ephelitus (Linnaeus). A, B, dorsal and ventral views of male form; C, D, dorsal and ventral views of female form. Notice the different sized abdomens.

In other cases the male may be smaller (dwarf male) than the female. For example, in the oriental cockroach (Blatta orientalis) the smaller male has longer antennae and a smaller abdomen. Among certain grasshoppers (Neoconocephalus) the smaller males lack caudal spines. The two sexes are very alike in carpenter moths (Prionoxystus robiniae), except that males are about half the size of females. In the horseshoe crab Xiphosura ("Limulus") the female is considerably larger than the male, and the male form possesses larger chelicerae which are modified as sexual claspers. The male of the shrimp Palaemonetes differs from the female in being smaller with a more slender rostrum, having the free part of the shorter ramus of the upper antennular flagellum longer in relation to the fused part, with somewhat shorter legs, and the carpus of second leg longer in relation to the chela. Younger female individuals resemble the male. In another shrimp, Xiphopeneus, the female's rostrum is somewhat longer than the male's; and in Hippolyte, still another, the male's body is more slender than the female's. The extreme examples of dwarf males are represented by many copepods, in which the male forms are sometimes diminuitive parasites upon the female's body.

2. Sexual Ratio

The sexual ratio among existing animals affords another clue for the identification of fossil forms. However, the knowledge of this field is rather poor.

In genetic theory the sexual ratio of animals may be 50:50. The reasoning is that, for example, in the human body the males have XY and

the female have XX sexual chromosomes. As a result of maturation, two kinds of sperm are formed in equal numbers with respect to these chromosomes. One kind having X (megasperm) and the other Y (microsperm). Only one kind of egg is formed, containing X. If an egg is fertilized by an X-bearing sperm, a female (XX) results; if by a Y bearing sperm, a male (XY). The proportion of fertilization of potential males and females is 1:1. But the facts do not conform to this hypothesis. The sexual ratio of many animals is more than 100: Human, 103; Cattle, 107.3; Pig, 111.8 (text-fig. 3); Mouse, 105; Pigeon, 115 (Ishibashi, 1938); Drosophila melanogastor, 300; and Man, 106 (Herskowitz, 1962). Although Ishibashi and Herskowitz give slightly different human sexual ratios, the fact remains that male individuals are more abundant than female.

Weight	Number	Male	Female	Male %
0-100 gr.	281	166	115	59.1 ± 1.98
101-300 gr.	114	65	49	57.0 ± 3.12
300- gr.	188	100	88	53.2 ± 2.45
Total	583	331	252	56.8 ± 1.38

Text-fig. 3: Showing pig sexual ratio at different growth stages. (After Parker, 1926, from Ishibashi, 1938).

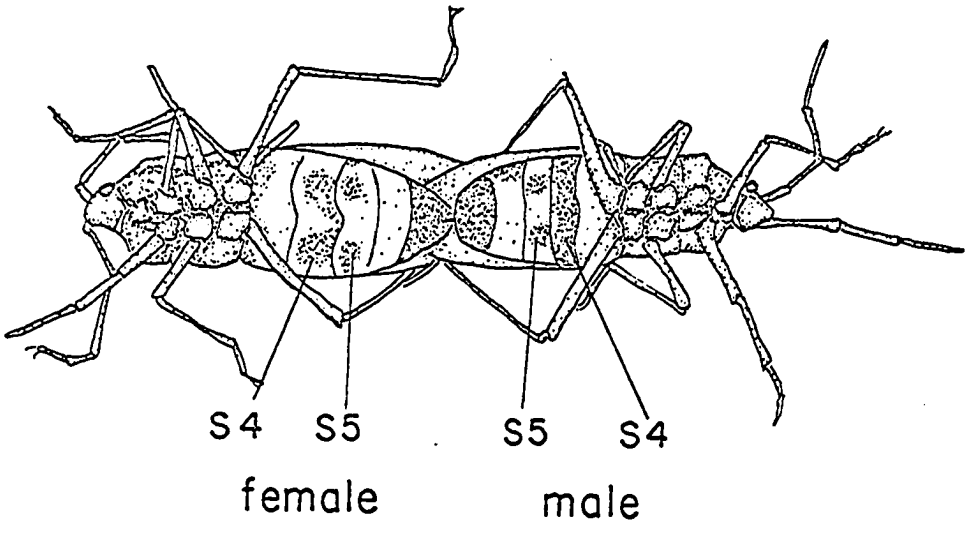
These results suggest that the ratio of the fertilization of XY is much higher than XX. The reason for this phenomenon is unknown, but the fact is that male individuals are more numerous than female.

It is not the subject of this paper to discuss the genetic sex determination of animals, but the author would like to point out that the sexual ratio is influenced by environment: such external factors as temperature, light, water salinity, food supply, or internal ones, such as sexual hormones and richness of acidic and alkalic media. These factors could affect the biochemical and biophysical reactions and directly or indirectly act as a partial sexual determinant. The slower motion of megasperm X than that of microsperm Y could be another important factor in sexual determination. Males are not universally more abundant than females, but under natural conditions the sexual ratio of any animal is predictable. In contrast, abnormal or experimental environments can cause the sexual ratio to vary randomly. The secondary reduction of male forms must also be considered. For example, many males die after copulation, are eaten by the female, killed fighting, or are inherently less viable, e.g., human males, and the result is an increase in the relative number of females in the species population.

3. Example of Animal Sexual Dimorphism

Sex determination in insects usually utilizes characteristics as shape of body, shape of antennae, size of eyes, color patterns and comparative length, or absence of wings. As an illustration, in the large milkweed bug, Oncopeltus fasciatus (Dallus), Lever (1966) has given the following criteria for identifying males:

1. They are smaller than the sibling female.
2. They lack the right and left lateral lobes on the dorsal surface of the fith abdominal segment (fifth tergite). The female's



Text-fig. 4: Sexual dimorphism of the milkweed bug, Oncopeltus fasciatus (Dallus), shown in copulation. S4, sternite no. 4; S5, sternite no. 5. (Redrawn from a photograph of Lever, 1966.)

lobes are readily visible when both pairs of wings are raised or removed.

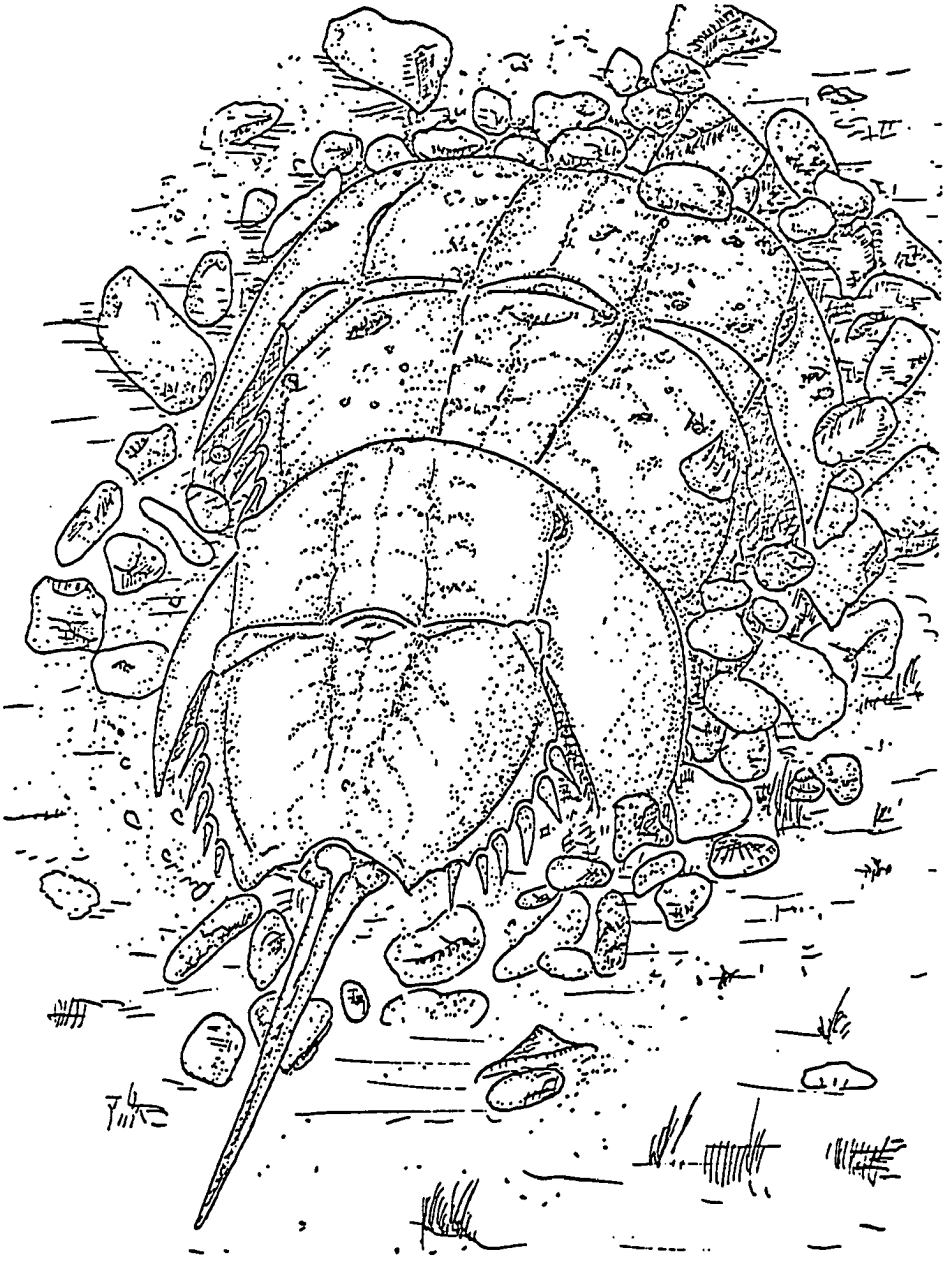
3. The posterior edge of the fourth plate on the ventral surface of the abdomen (fourth sternite) is rounded. The female's is triangular and tapers posteriorly (text-fig. 4).

4. The last dorsal segment of the male's abdomen (the pygidium) is rounded and shiny. The female's is triangular, dull and cleft.

Text-fig. 4: Sexual dimorphism of the milkweed bug, Oncopeltus fasciatus (Dallus), shown in copulation. S4, sternite no. 4; S5, sternite no. 5. (Redrawn from a photograph of Lever, 1966.)

In the decapod crustacean, Callianassa, there is dimorphism of the chelipeds. The male has a rather large major cheliped, granular along the proximal lower edge of the carpus, lower edge of the merus and over the entire ischium; the propodus and carpus are about equal in length, twice as broad as the merus and more than three times as broad as the ischium; the merus has a strong tooth on the lower proximal border; whereas the major cheliped of the female is weaker and not granulated; the propodus and carpus are proportionally shorter than those of the male and the merus lacks a tooth on the lower proximal border.

The horse-shoe crab, Xiphosura, shows sexual dimorphism in the chelae, the males having special graspers. The crabs spawn during the month of May, or in the Spring whenever weather is conducive. The males respond first, awaiting the arrival of the females in the shallow



Text-fig. 5: Mating of the horse-shoe crab, Xiphosura polyphemus (Linn). The anterior one is the female and the posterior the male.

(From a photograph by Patten, in Caster, 1938.)

water along the beaches. Generally only one male attaches with his "fist-and-thumb" chela to a female, but a female simultaneously spawning with two or more males is not uncommon. Spawning occurs on the high tides of the new full moon. As each female makes her way to the beach she is accompanied by a male clasping the posterior margin of the female abdomen with specialized claws. At the water's edge she digs a shallow nest in the sand, often practically burying herself, and deposits the clutch of eggs in the shallow depression, where they are fertilized by the spermatozoa washed over the eggs by the waves. The female moves on to make several nests during a single tide. Occasionally a male may remain coupled to the female throughout the year, from one spawning season to the next (text-fig. 5) (Shuster, 1950).

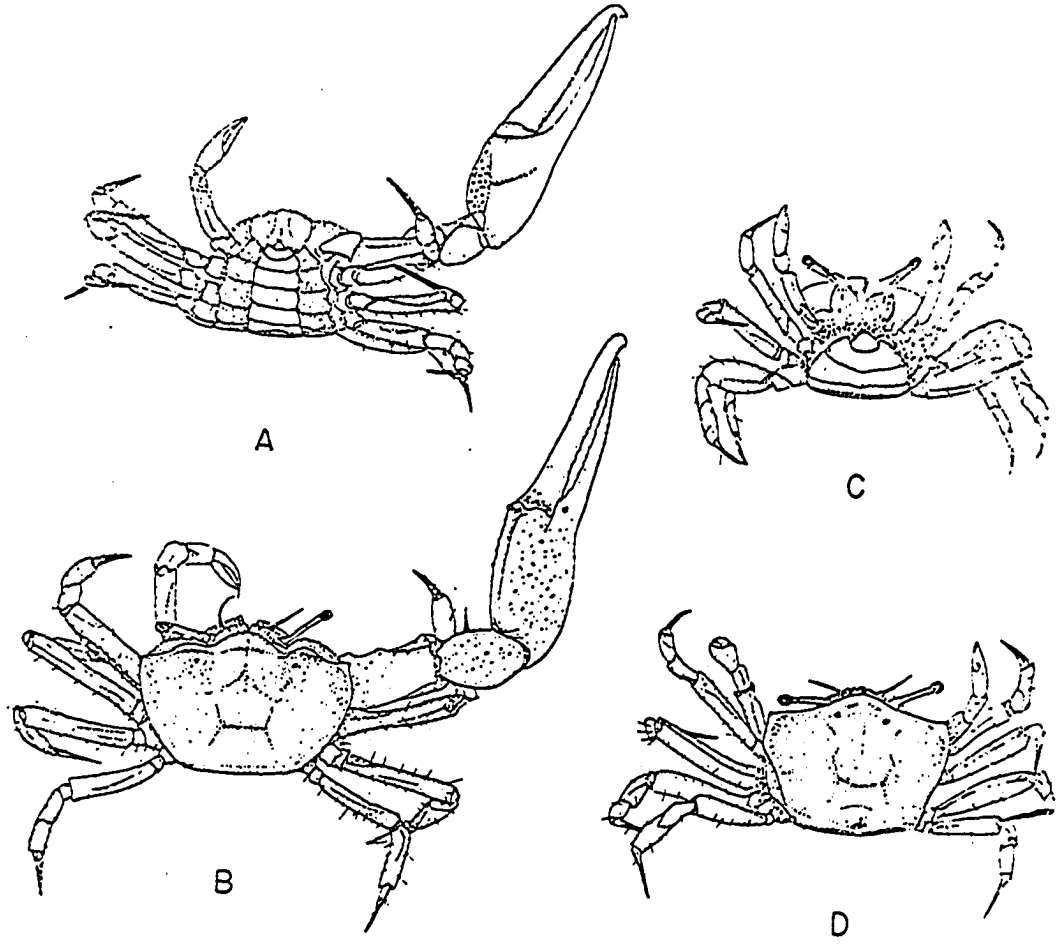
The sand fiddler crab, Uca pugilator, is commonly found along the East Coast of North America. The largest male individuals are more than 16 mm. in length, and the female is slightly smaller. They occur in countless numbers on the sandy and muddy beaches bordering on the tidal creeks (text-fig. 6). The chelipeds of the male are unequal in size, and the abdomen is smaller. In females the chelipeds are equal and

---

Text-fig. 5: Mating of the horse-shoe crab, Xiphosura polyphemus (Linn). The anterior one is the female and the posterior the male.
(From a photograph by Patten, in Caster, 1938.)

---

smaller, and the abdomen is larger and rounded. Intersexual forms having large abdomen and unequal chelipeds are rare occurrences. The carapace of the male is dull, light-purplish or grayish-blue and of varying shape,



Text-fig. 6: Showing sexual dimorphism of Uca pugilator (Bosc). A,B, ventral and dorsal views of male form; C,D, ventral and dorsal views of female form. Notice the difference in size of body, chelipeds, and abdomen in the two sexes. (From photographs.)

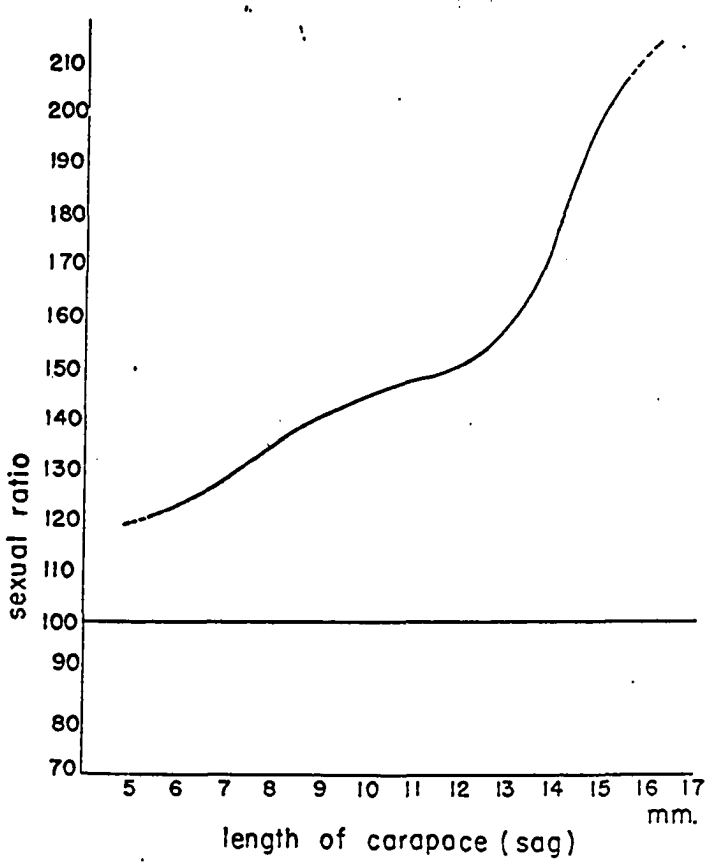
or with irregular markings of brown or dark grey; the female is lighter than the male.

The writer collected about 3000 Uca pugilator individuals during the week of July 6-12, 1966, at Beaufort, North Carolina, near the Duke Marine Laboratory. Among these the smallest specimens are about 5 mm., the largest male form is 17.5 mm., and the female is rarely 16.0 mm. long (carapace sag.). The sexual ratio of the smaller sized forms is 120; of the medium sized, 148.3; and of the large ones, 200.

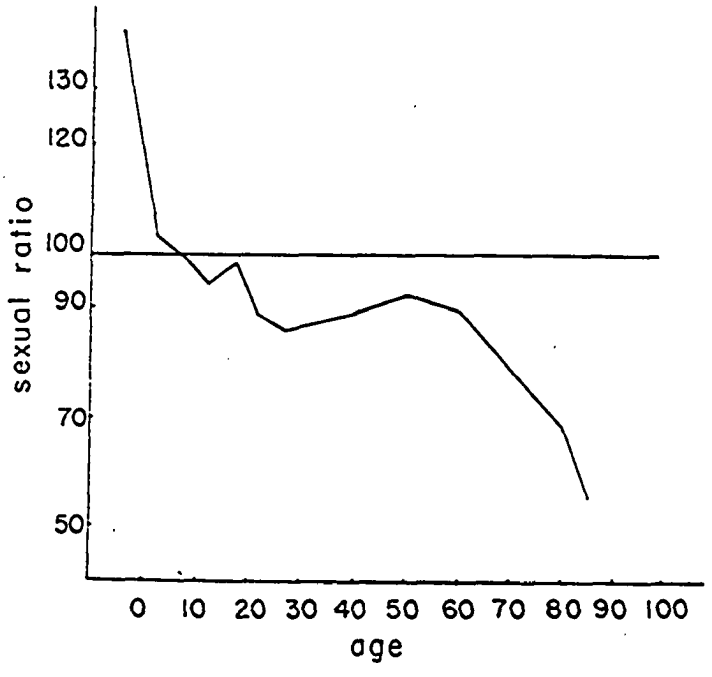
Text-fig. 6: Showing sexual dimorphism of Uca pugilator (Bosc). A,B ventral and dorsal views of male form; C,D, ventral and dorsal view of female form. Notice the difference in size of body, chelipeds, and abdomen in the two sexes. (From photographs.)

Although the sexual ratio of this animal would at first seem to be chaotic, the explanation no doubt lies in the fact of near-shore collecting. Under the sampling conditions, quite probably the population of sexually juvenile forms comes closer to representing the true sexual ratio, whereas the variable sexual ratios of the adult forms are due to the females usually being very inactive and commonly hidden, and active males are caught in the sampling.

Von Bälz's (1911) investigation indicates that the human sexual ratio of England is 103.6; Italy 108; Russia 105.4; Germany 105.2; France 104.6; Spain 108.3; and Japan 105. Parker's (1915, 1926) report on the juvenile sexual ratio of the embryonic stage of man is extremely high (120-140). The ratio decreases from infancy to adulthood (text-fig. 8).



Text-fig. 7: Sexual ratio of Uca pugilator (Bosc).



Text-fig. 8: Human sexual ratio. (After Parker, 1913, from Ishibashi, 1938.)

Text-fig. 7: Sexual ratio of Uca pugilator (Bosc).

Text-fig. 8: Human sexual ratio. (After Parker, 1913, from Ishibashi, 1938.)

In the United States the sexual ratio averages about 103 from 1850 to 1959 (Year Book, 1961), and the birth and death ratios are 105.4 and 130.4 respectively (World Almanac, 1958). The birth ratio of the male population is much higher and the death rate of male population is also higher than that of the female.

4. Suggestions for Identification of Sexual Differences in Trilobites

a. Sexual radio -- As discussed above, statistical studies often show two morphologically differentiated groups in the same species of trilobites. It would seem in conformity with the usual condition in nature, that the larger group of specimens is male and the smaller one female.

b. Body size -- In general, the group which has the larger mean size is probably female and the group of smaller mean size male. But if the animal is strongly armored or bears prominent prosopon, the

situation appears to be reversed: then, the group of the larger mean size conforms statistically to the male data, and the group of smaller mean size, to the female.

c. Prosopon -- Spinous or heavily armored forms are judged to be male, and those without or only slightly armored to be female.

This correlation is derived statistically and represents probability rather than demonstratable truth, since the sexual organs of trilobites are unknown. Biocoenosis, thanatocoenosis, and sedimentologic history need careful examination for each association, lest these factors distort the true population statistics.

II. ONTOGENY OF POLYCHAETES, CRUSTACEANS, AND MEROSTOMES

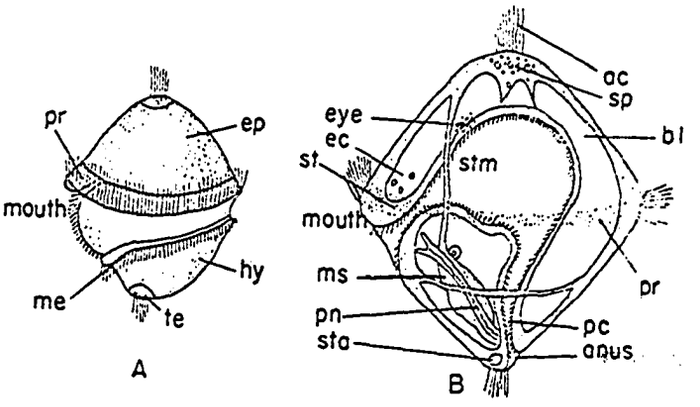
1. Ontogenetic Development of Polychaetes

The embryos of polychaetes (Nereis, Tomopteris, Scoloplos, etc.) develop by means of spiral cleavage and gastrulation to produce the larvae. The embryo at this stage assumes a top-shape and leads a purely pelagic life, moving by bands of cilia that encircle the body. This is the trochophore stage. The fully developed trochophore is divided into two parts by an equatorial ring; an episphere above, and an hyposphere below (text-fig. 9). The hyposphere consists of the metatroch, neurotroch, telotroch, prepygidial growth zone, and the anal region or pygidium. The prepygidial growth zone eventually forms serially all of the trunk segments of the body.

Additional development takes place as the trochophore metamorphoses into adult body form. The most conspicuous feature of metamorphosis is the gradual lengthening of the generative zone due to the formation and development of trunk segments. The segments develop almost simultaneiously from anterior to posterior, between metatroch and pygidium. These constitute the primary or larval somites. The number of primary somites varies considerably from taxon to taxon within the Annelida.

The sequence of segments which is serially added to the larval segments comprises the secondary segments or post-larval somites. They are generated by the prepygidial growth zone.

Each somite develops two coelomic compartments. The formation of



Text-fig. 9: A, External view of the trochophore of Polygordius, showing prototroch, metatroch, and telotroch. B, Internal structure of generalized annelid trochophore. (After Dawydoff and Shearer from Barnes, 1963). ac, apical tuft of cilia; bl, blastocoel; ep, episphere; ec, ectomesoderm; ms, mesodermal bands, me, metatroch; pr, prototroch; pc, proctodeum; pn, protonephridium; sp, sensory plate; st, stomodeum; stm, stomach; sta, statocysts; te, telotroch.

the segments are marked externally by development of setal sacs and setae. Also each of the early segments is commonly ringed by a girdle of cilia.

In the espispheric region, which originally forms the major part of the trochophore, the cells of the apical plate form the prostomium and the "brain"; concomitantly the mesodermal tissue moves forward and invades the prostomium. The mouth region may fuse with the first or first and second trunk segments from the peristomium. This process is commonly seen in Nereis, Tomopteris, Pisione, and in the sabellids and serpulids. These differences in peristomium origin indicate that the peristomia of different polychaete groups are not necessarily homologous.

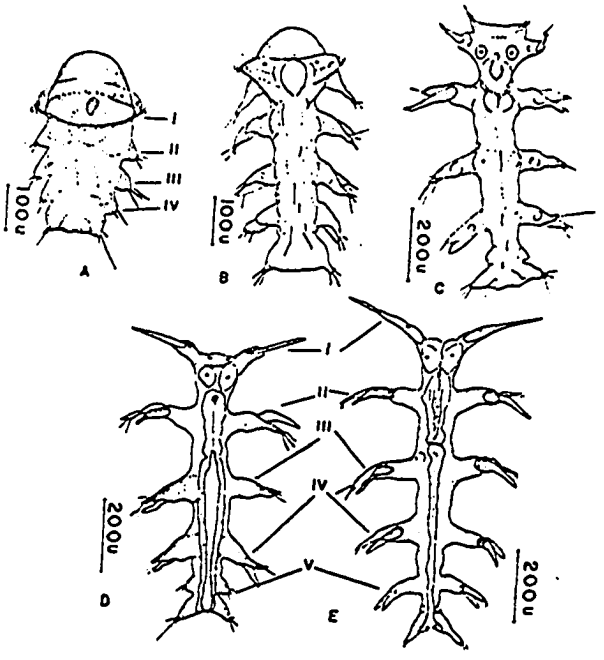
Text-fig. 9: A, External view of the trochophore of Polygordius, showing prototroch, metatroch, and telotroch. B, Internal structure of generalized annelid trochophore. (After Dawydoff and Shearer from Barnes, 1963). ac, apical tuft of cilia; bl, blastocoel; ep, episphere; ec, ectomesoderm; ms, mesodermal bands, me, metatroch; pr, prototroch; pc, proctodeum; pn, protonephridium; sp, sensory plate; st, stomodeum; stm, stomach; sta, statocysts; te, telotroch.

The elongated metamorphosing larvae remain planktonic for varying lengths of time, but generally at the time of settling there are six or seven setae-bearing segments. However, the larvae of Ophelia are free-swimming only until three setae-bearing segments have developed.

A. Examples of the ontogenetic development of polychaetes

It is quite misleading to generalize too widely upon polychaete ontogeny since many variables are operative: e.g., varying segmental processes in pelagic and benthonic larvae and the mode of prostomial metamorphosis. A few examples of these differences are summarized below: -

Tomopteris helgolandica Greeff: The ontogenetic development of Tomopteris helgolandica was studied by Åkessen (1962). The animal is holopelagic throughout life. In adulthood the body is from 50 to 100 mm. in length, of which the larger specimens are mostly female. The fertilized egg develops spiral cleavage; gastrulation is finished in about 28 hours; at about the third day the embryo is developed into a trochophore; late in the third day, four segments are simultaneously delinated as lateral protrusions separated by intersegmental grooves, and four pairs of parapodial rudiments are seen. The parapodia differentiate into dorsal and ventral branches and bear long bristles. Late in the fifth day the fifth segment appears as the first sign of activity of the prepygidial growth zone. For a surprisingly long time this fifth segment is the only one which buds off from the growth zone. From the fifth day the morphology of the larva changes very slowly with respect to the middle and posterior parts of the trunk region and the pygidium. During this period the prototroch and first segment are forced toward the apical pole along with the previously equatorial line (text-fig. 10).



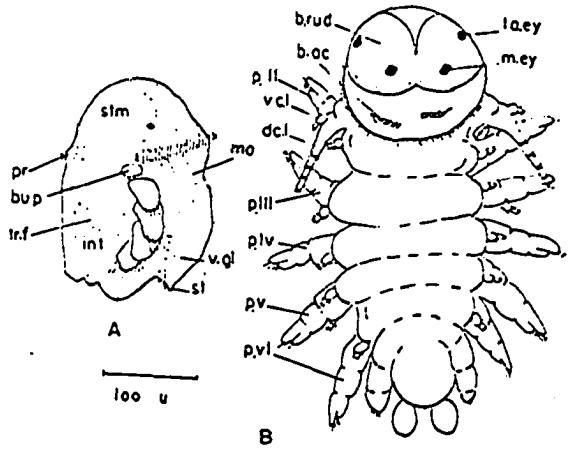
Text-fig. 10: Embryonic development of Tomopteris helgolandica Greeff. A, 4-day embryo; B, 5-day embryo; C, 6-day embryo; D, 7-day embryo; E, 11-day embryo. Note the development of primary somites (I-IV), secondary somite (V), and forward migration of the prototroch and the first pair of setigerous cirri. (Drawn from photographs of Akesson, 1962.)

Text-fig. 10: Embryonic development of Tomopteris helgolandica Greeff. A, 4-day embryo; B, 5-day embryo; C, 6-day embryo; D, 7-day embryo; E, 11-day embryo. Note the development of primary somites (I-IV), secondary somite (V), and forward migration of the prototroch and the first pair of setigerous cirri. (Drawn from photographs of Åkesson, 1962.)

The larva differentiate very little beyond this stage through the ninth day. By the fifteenth day, the tentacles bud off and the seventh segment appears. At the 9-10 segmental period the tentacles become hollow and connect with the general coelom.

The initial stage of segmentation of the animal first becomes visible in the ectoderm and not in the mesoderm. The first segmental indications are first visible in the lateral ectoderm where the cells arrange themselves in four bulbous structures on each side. The four bands represent synchronously developing primary larval segments. There is, however, a fifth larval segment, the formation of which is delayed at least 24 hours after the fourth primary segment is completed.

Pisione remota (Southern): Pisione remota has a very interesting larval developmental pattern. It is very much like a Lower Cambrian trilobite, (p.173). The animal is errant in life with planktonic larva early and benthonic later. Åkesson (1961) divided the life period into two stages: planktonic and bottom stages, and eight substages, as listed below*.

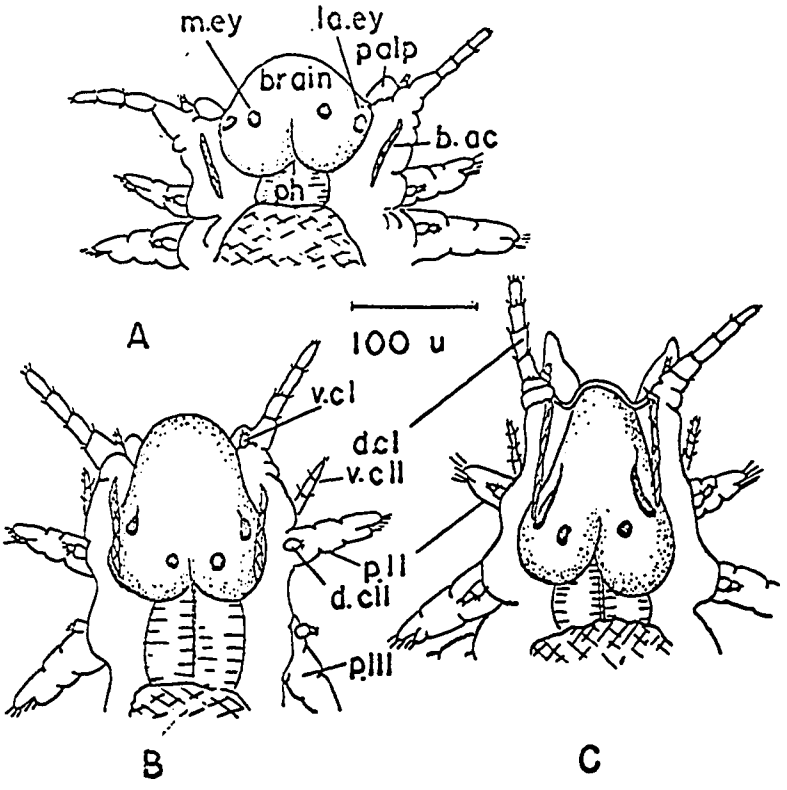


Text-fig. 11: Planktonic larvae of Pisione remota (Southern). A, a young metatrochopore; B, older stage, not yet ready to metamorphose. b.rud, brain rudiment; b.ac, buccal aciculum; dc.1, dorsal cirrus of the buccal segment; dc. II, dorsal cirrus of the second segment; int, intestine; la.ey, median eye; p. II-IV, parapodium; ph, pharynx; mo, mouth; pr, prototroch; stm, stomadaeum; tr.f, transversal fold; vc. I-II, ventral cirrus of the first and second segment; v.gl, ventral gland. (After Åkesson, 1961.)

* As indicated on text-figures 11 and 12, Åkesson shows this annelid as possessing slender appendages which appear to be both segmented and in part biramous. Further study of this condition is essential, for if this is not pseudo-segmentation of the appendages (e.g., as in the Onychophora), Pisione may lie extremely close to the transition from annelids to arthropods in this respect, as it appears to lie in associated cephalic features and other aspects of early larval growth.

1. Planktonic stage (text-fig. 11). A) Larva with 3 pairs of setigerous parapodia; the appendages of the buccal segment not visible; one pair of eyes. B) Larvae with 3 to 4 pairs of parapodia; the buccal appendages are visible as rounded protrusions; one pair of eyes. C) Larvae with 6 to 7 segments; the dorsal cirri of the buccal segment are longer than the parapodia proper; subulate ventral cirri have developed in the first setigerous segment; two pairs of eyes. D) Larvae with 8 segments; the persisting prototroch is somewhat displaced laterally through the forward migration of the buccal parapodia. These larvae are ready for metamorphosis.

Text-fig. 11: Planktonic larvae of Pisione remota (Southern). A, a young metatrochopore; B, older stage, not yet ready to metamorphose. b.rud, brain rudiment; b.ac, buccal aciculum; dc.1, dorsal cirrus of the buccal segment; dc. II, dorsal cirrus of the second segment; int, intestine; la,ey, median eye; p. II-IV, parapodium; ph, pharynx; mo, mouth; pr, prototroch; stm, stomadaeum; tr.f, transversal fold; vc. I-II, ventral cirrus of the first and second segment; v.gl, ventral gland. (After Åkesson, 1961.)

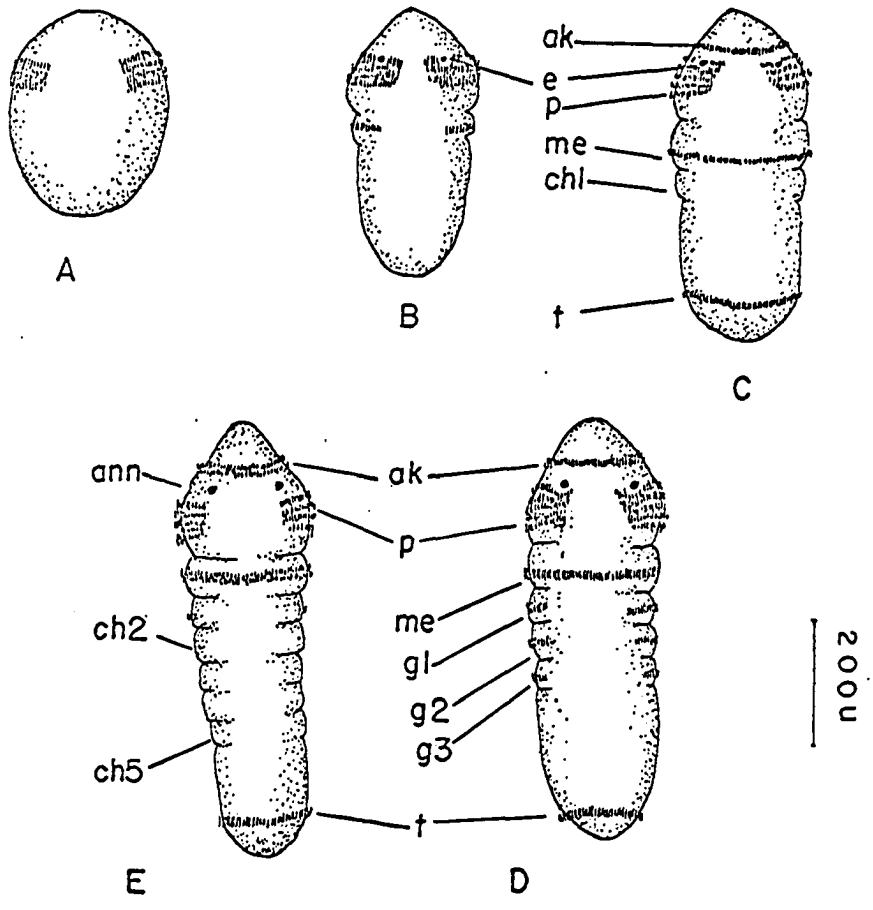


Text-fig. 12: Three larvae of Pisione remota (Southern) at different stages of metamorphosis. Note the forward migration of the body segments and the elongation of the lateral eyes. For explanation see text-fig. 11. (After Åkesson, 1961.)

2. Bottom stage (text-fig. 12). E) Larvae with 8 segments; the prototroch is vestigial or has disappeared. In a dorsal view the brain is circular with 4 eyes at approximately the same level. F) Larvae with 8 segments; two pairs of eyes, one in the posterior of the elongated brain, the other, lateral and elongates (text-fig. 12B, C). G) Larvae with 8 segments; the still more elongated brain extends to the posterior margin of the third setigerous segments. The two pairs of eyes are now located in the anterior and posterior region of the brain respectively. H) Larvae with 10 segments; the anterior end now has the adult organization. The anterior, originally lateral, pair of eyes is more or less reduced.

Text-fig. 12: Three larvae of Pisione remota (Southern) at different stages of metamorphosis. Note the forward migration of the body segments and the elongation of the lateral eyes. For explanation see text-fig. 11. (After Åkesson, 1961.)

Scoloplos armiger Müller: The embryology of Scoloplos armiger was studied by Anderson (1959). The yolky eggs of Scoloplos armiger are are layed in gelatinous cocoons, and develop by spiral cleavage and gastrulation to produce a yolky trochophore, which then developes 12 primary segments in strict succession. Ciliated bands occur, though development is nonpelagic. Segment-formation ceases after 8 days and the embryo hatches and metamorphoses into a free pre-adult, cilia being developed last and yolk resorbed. Additional segments, the secondary ones, are now added (text-fig. 13).



Text-fig. 13: The early embryonic development of Scoloplos armiger Müller. A, unfertilized egg; B, early 4-day embryo, dorsal view; C, late 5-day embryo; D, late 6-day embryo; E, early 7-day embryo. Note the continuous development of the body segments. ak, acrotroch; ann, post-pro-prostomial antennules; ch. 1,2,5, chaetiger 1, 2, 5; e, eye; g, 1,2,3, gastrotroch of chaetigers 1, 2, and 3; me, metatroch; p, prototroch; t, telotroch. (After Anderson, 1959.)

Anterior to the first primary segment lies the prostomium and mouth region derived from the body, or episphere, of the trochophore. Posterior to the primary or secondary segments is a prepygidial growth zone, followed by a terminal pygidium. The primary and the secondary segments have a similar origin and both are formed before ectoderm; each segment contains a pair of hollow mesodermal somites, usually of "4d" origin; this is the mesoderm.

Arenicola cristata Stimpson: Arenicola cristata inhabits muddy sand at the extreme low water line. The surface of the inhabited area is marked by a large (2" to 3" in diameter) low black cone. In life the body is deeply yellowish-green to dark-purple, with 11 pair of branchiae and 6 pair of rudimentary parapodia in front of a long, non-appended pygidium. It attains a length of 8 to 10 inches.

Text-fig. 13: The early embryonic development of Scoloplos armiger Müller. A, unfertilized egg; B, early 4-day embryo, dorsal view; C, late 5-day embryo; D, late 6-day embryo; E, early 7-day embryo. Note the continuous development of the body segments. ak, acrotroch; ann, post-pro-prostomial antennules; ch. 1,2,5, chaetiger 1, 2, 5; e, eye; g, 1,2,3, gastrotroch of chaetigers 1, 2, and 3; me, metatroch; p, prototroch; t, telotroch. (After Anderson, 1959.)

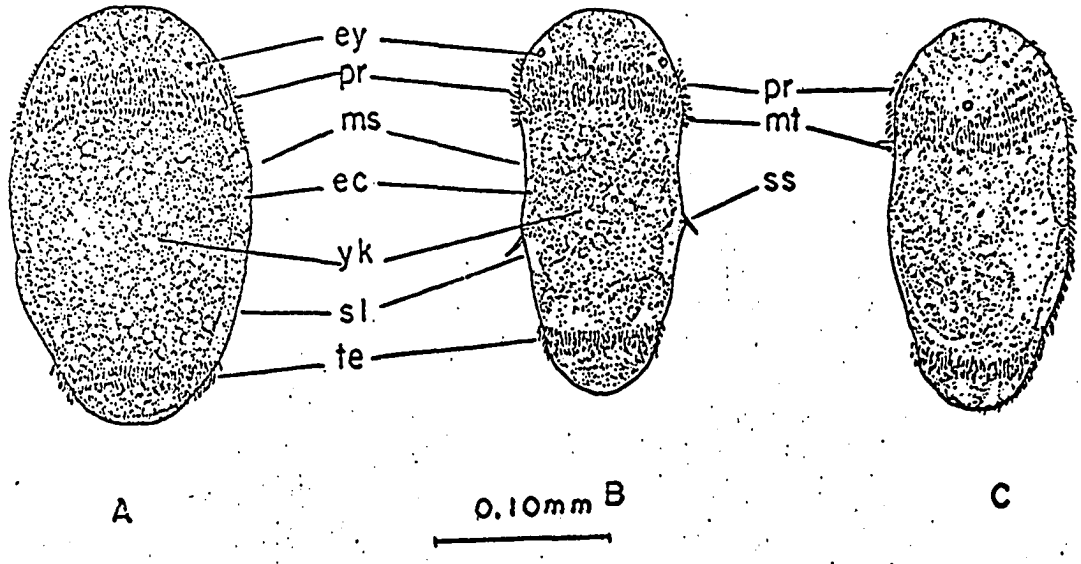
Eggs are deposited in a large (5 inches to 2 feet in length), spherical, cucumber-shaped gelatinous mass, which is attached to the upper end of the bottom by a gelatinous filament. The writer had an opportunity to study the ontogenetic development of the animal during early September

to December, 1967, at the Duke Marine Laboratory, Beaufort, North Carolina. The following is a brief discussion of the results of this research.

The gelatinous egg cases of the animal were collected during mid-September to the end of October from Bird Shoals, near Duke University Marine Laboratory and taken to the Laboratory in jars of sea water, where the mass containing developing embryos was separated into finger-bowls containing filtered sea water which was changed daily. Here the embryos hatched from the jelly and entered approximately 20 hours of free-swimming period, after which they built muddy tubes from a small amount of muddy sand added to each bowl. Diatoms liberated from the disintegrating jelly mass served as food for the developing larvae.

The early ontogenetic development of the animal is divisible into four stages and four ecological phases. These stages and phases almost parallel each other, except the Free Swimming Phase is developed within the metatrachophore stage (text-fig. 16). A brief description of the development of the animal follows:

Embryo-Trochophore stage (text-fig. 14A-C, and text-fig. 15). The eggs are brownish-yellow, opaque, oval, and about 0.13 to 0.15 mm. in diameter. The fertilized eggs develop into embryos about 15 hours after field collecting. The embryos, rotating within the vitelline membrane, are nearly the same size as the eggs, and are covered with cilia. After approximately 30 hours, the trochophores are hatched out from the vitelline membrane, and are about 0.20-0.22 mm. in length, and about 0.10 mm. in width, with well-defined proto-, narrow meta-, broad neuro-, and telo-trochs. A pair of red eye-spots is located laterally



Text-fig. 14: Early metatrochophore of Arenicola cristata Stimpson, showing the process of segmentation. A, note the ectodermal segmentation before formation of mesoderm; B,C, dorsal and side views of a larva with a single pair of setae, ec, ectoderm; ms, mouth segment; mt, metatroch; pr, prototroch; sl, first segment; ss, first pair stae; yk, yolk; te, telotroch.

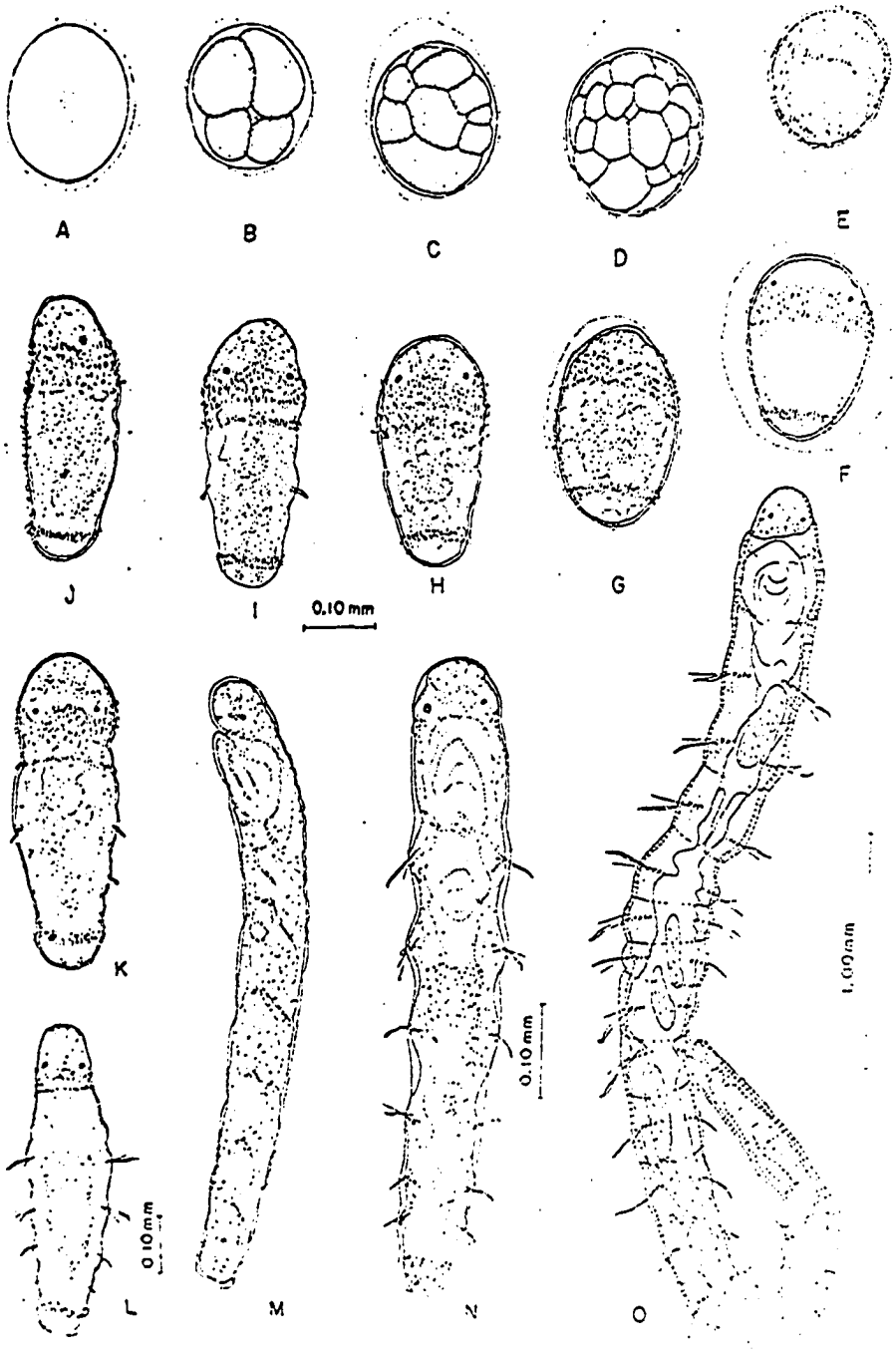
(All drawings were from photographs; the animals were slightly flattened by the cover-glass of the slide mount.)

Text-fig. 14: Early metatrochophore of Arenicola cristata Stimpson, showing the process of segmentation. A, note the ectodermal segmentation before formation of mesoderm; B,C, dorsal and side views of a larva with a single pair of setae. ec, ectoderm; ms, mouth segment; mt, metatroch; pr, prototroch; s1, first segment; ss, first pair stae; yk, yolk; te, telotroch. (All drawings were from photographs; the animals were slightly flattened by the cover-glass of the slide mount.)

at the margin of the prostomium. The larvae, having one or two segments, generally pass through a short free-swimming phase, then attach on a small piece of animal skeleton or alga to enter a 6 to 7 day pseudoplanktonic phase. The pseudoplanktonic life history is demonstrated by both laboratory experiments and planktonic net trawling. The larvae are quite light-positive, and if a piece of alga is thrown into the finger bowl, the larvae will quickly attach to it and secrete a small gelatinous body cover.

Metatrochophore stage (text-fig. 15, H-L). The larvae at this period have one oral and one to six setal segments and vary between 0.25-0.75 mm. in length. The first segment appears, without setae, shortly after the trochophore hatches out from the vitelline membrane; it is well-defined by folded ectoderm. The six pairs of appendages or segments are added sequentially over a period of 8 days.

Early juvenile stage (text-fig. 15, M-N). The body of the animal contains 7 to 17 setal segments and about 1.00 to 2.30 mm. in length.



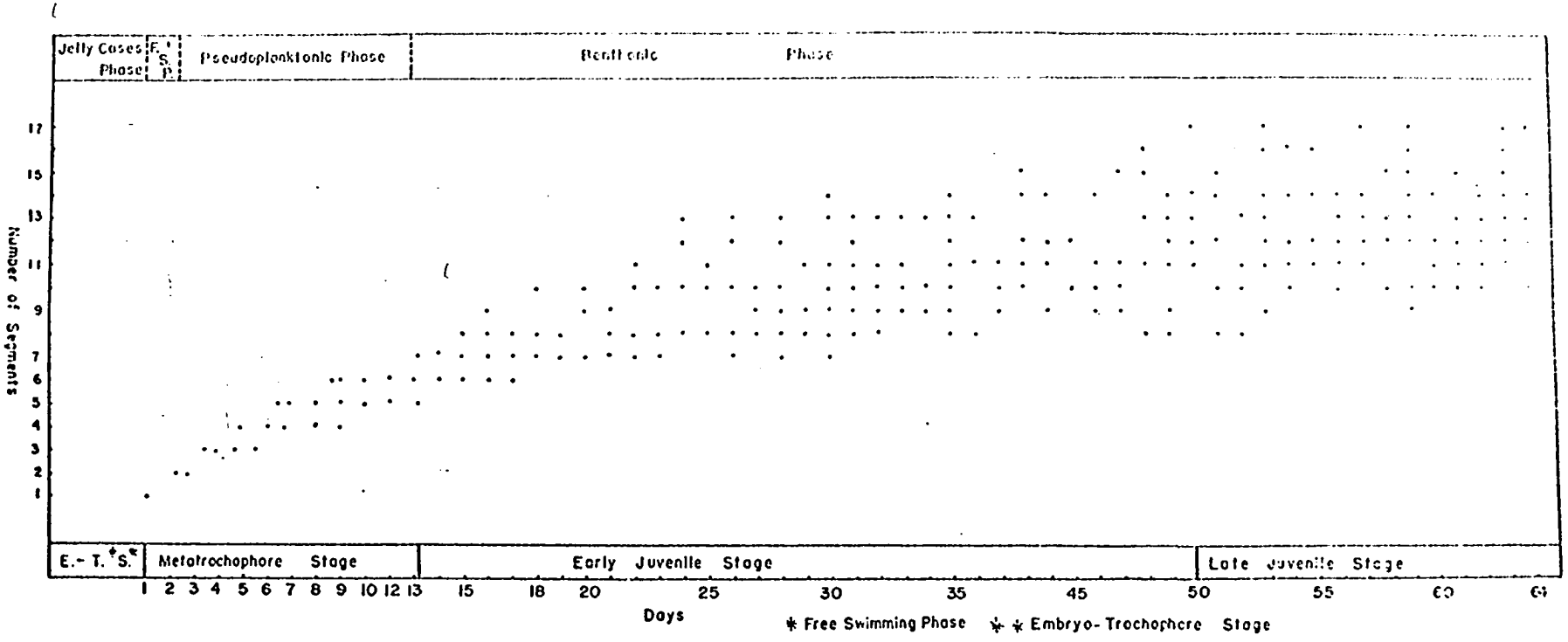
Text-fig. 15: An ontogenetic sequence of Arenicola cristata Stimpson. A, unfertilized egg; B,C,D, cell cleavage, showing 4,16,32 cella stages; E, an early embryo; F,G, top and side views of trochophore; H-L, a few different sized metatrochophores, note the segmental process; M,N, side and dorsal views of an early juvenile; O, a late juvenile. (All drawings made from photographs.)

Text-fig. 15: An ontogenetic sequence of Arenicola cristata Stimpson. A, unfertilized egg; B,C,D, cell cleavage, showing 4,16,32 cells stages; E, an early embryo; F,G, top and side views of trochophore; H-L, a few different sized metatrochophores, note the segmental process; M,N, side and dorsal views of an early juvenile; O, a late juvenile. (All drawings made from photographs.)

The 7th segment appears three and one-half days after the 6th segment has been completed, and growth continues; the 17th segment being completed approximately 30 days later. The first 17 segments are each with well developed appendages. The mode of life of the animal from the early stage of this period is burrowing or living in a muddy sand tube.

Late juvenile stage (text-fig. 15 O). In this period the larvae add the rudimentary segments, i.e., the segments without any appendages behind the 17th segment. The prostomium is proportionally reduced in size and the 7th to 17th appendages are formed into 11 pairs of gills. The length of the animals is more than 3.00 mm.

Text-fig. 16: Showing the growth stages and ecological phases during the ontogenetic development of Arenicola cristata Stimpson. Note the segmental process ceases from 9th to 13th day.



Text-fig. 16: Showing the growth stages and ecological phases during the ontogenetic development of Arenicola cristata Stimpson. Note the segmental process ceases from 9th to 13th day.

B. The Prostomium

The prostomium is the "head" of the polychaete. It originates from the episphere, or in front of the prototroch of the trochophore, and is composed of mouth, eyes, palps, and nuchal organ. The prostomium is the presegmental region except that mesodermal bands grow forward from the segmental zone into this region on each side to fuse in front of the mouth, and paired sacs may arise within them. Some morphologists have maintained that the occurrence of these sacs lends support to the view that the prostomium is derived from a number of segments which have been reduced by cephalization. The suggestion that the prostomium might contain as many as three segments, however, first came from the studies of the brain, which in many worms has the appearance of being made up of three pairs of ganglia closely fused. Opponents of this idea argue that the brain is functionally separable into "fore", "mid", and "hind" brain regions owing to the correlation centers associated with the paired sense organs which are borne on the prostomium. These are the tactile, and possible chemosensory, antennae, palps, eyes, and chemosensory nuchal organs, none of which has any obvious counterpart on the succeeding segments. In studying the development of Scoloplos armiger, Anderson (1959) concluded that there was no evidence for the view that there are vestiges of any segments in front of the first definitive trunk segment; that the brain and the circumoesophageal commissures are presegmental structures; and that the forward growth of the mesoderm and the appearance of the cavities within it are secondary developments. The ganglionic centers occur in the prostomium and they can be presumed to have evolved in situ in association with paired

prostomial sense organs, and not as the ganglia of cephalized trunk segments; there is no evidence for incorporation of segmental ganglia into the polychaete brain in the manner of arthropods.

The peristomium is formed by a fusion of more than one trunk segment immediately behind the prostomium. In Nereis and Tomopteris the peristomium is formed by two trunk segments, since it bears two pairs of cirri on each side similar to those of the parapodia farther back. Pisione has three trunk segments incorporated with the prostomium. The more posterior of the peristomial cirri are innervated by a parapodia ganglion just beneath the bases of the cirri, and are secondarily connected to another ganglion on the circumoesophageal commissure at the same horizontal level; but these parapodial ganglia remain distinctly separated from the brain, even when their individuality is externally masked by a loss of their parapodia in the adult worm. Anderson goes on to say that we can at present only conclude that there is certainly no evidence whatever for the view that any part of the brain, circumoesophageal commissures, or the mouth region, is derived from the most anterior segment by cephalization, and that, on the contrary, the brain and all the structures that it directly innervates, such as the palps and antennae, are presegmental in structure. Structures such as the peristomial cirri, which are manifestly derived from the most anterior segments, are always innervated from ganglia which retain their identity and remain separate from the brain.

C. Segmentation Problems

In a series of papers Iwanoff (1928, 1933, 1944) discusses the primary and secondary segmentation in articulates. The primary segments, or larval segments, which form the main part of the functional embryo, all appear simultaneously and are derived from the ectodermal activity. The secondary segments, or post-larval segments, which give rise to most of the adult body, are budded off in a strict succession from the prepygidial growth zone and primitively contain nephridia and reproductive organs. This heteronomy in segment formation is found not only among the polychaetes but also in other phyla such as arthropods, enteropneusts, and chordates. The number of primary somites varies considerably within the polychaete annelids, but seems to be distinct in separate families. Also among the arthropods it has been possible to distinguish primary and secondary somites. Iwanoff demonstrated the presence of four postoral primary somites in the merostomes and has given cogent reasons to believe that the same number of primary somites occurs in Chelicerata and Trilobita, whereas the Crustacea evidently have only two primary somites. For these reasons, Iwanoff comes to the conclusion that the varying number of primary somites suggests a polyphyletic origin of the arthropods. This view has been accepted by several writers: Remane (1949), Snodgrass (1938), Størmer (1944), and Beklemischew (1952). It has been rejected by Manton (1949), Tiegs and Manton (1958), Anderson (1959), and Åkesson (1962), who argue that the different numbers of primary somites in polychaete larvae, heteronomous or nonheteronomous, can be interpreted best in terms of functional specialization enhancing the efficiency of the growing

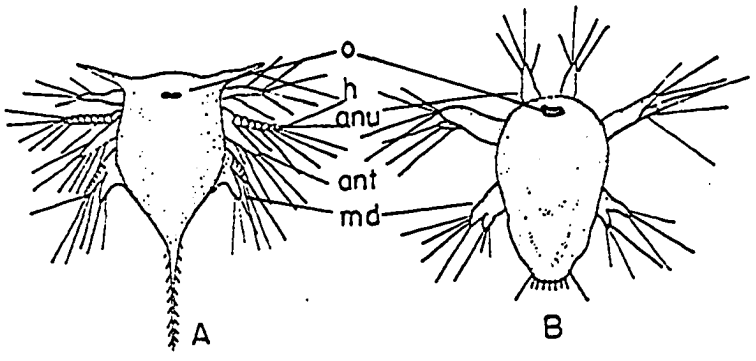
organism, whether pelagic or nonpelagic.

Returning to the condition found among the polychaetes, a few examples of the ontogenetic development of polychaetes have been here presented to demonstrate the morphologic variations of the prostomium and heteronomous and non-heteronomous segmental processes of the animals. Tomopteris helgolandica is an heteronomous polychaete, in which three primary segments simultaneously appear between the prototroch and the telotroch by segmentation of the ectoderm, and the secondary segments are developed from the prepygidial growth zone. The same process is also found in Eunice kobiensis (Åkesson, 1967), the Nereidae, Serpulidae, etc. Non-heteronomous or partly heteronomous forms are illustrated by Scoloplos amiger (Anderson, 1959), Halploscoloplos fragilis (Åkesson, 1961), Polygordius, etc. which are without any distinction between primary and secondary segmentation; the segment formation in these annelids takes place evenly from anterior backward, with the mesoderm segmenting before the ectoderm. However, these forms do have a shallow segmental break between certain segments, but the segmenting first appears in the mesoderm; it is not like heteronomous segmentation, which first appears on the ectoderm.

The observation on the segmental process and the mode of life of Arenicola cristata and Axiothella muscosa has led to the conclusion that Iwanoff's theory is still tenable. These observations do not support Manton, et al. that the heteronomic segmental process is merely a functional response to the needs of the larva during planktonic life. In the larval development of Arenicola cristata, the early trochophore has a short free-swimming period (during the 1st and 2nd segmental stage)

but lacks heteronomy; Axiothella mucosa (Bookhout, 1949) exhibits heteronomy (3 or 4 primary segments) but no planktonic stage, and in these the ectodermal segmentation precedes mesodermal (text-fig. 14A). The functional response to the needs of the larvae does not seem to be a convincing argument against Iwanoff's theorgy. The presence or absence of heteronomy among polychaetes seems rather to be a fundamental condition, and probably indicates separate annelidan origins for derived groups such as the different arthropod classes or mollusks.

Segrove (1941) postulated that the primitive (hypothetical) polychaete produced a large number of small eggs which developed into fully ciliated larvae. These larvae were pelagic and fed on the microplankton for a long time before undergoing metamorphosis. The cilia were mainly for locomotion and perhaps to a much lesser extent for feeding. Another line, characterized by benthonic larvae, developed from this hypothetical type. They produced a small number of large, yolk-laden eggs. The larvae developing from these eggs depend on the yolk and not on an external food supply, hence the feeding and locomotor ciliary apparatus was suppressed. In some of the benthonic types, however, cilia seem to have been retained for a respiratory function. Monton (1949) and Anderson (1959) have also both argued that forms with benthonic mode of life, producing few, large yolk eggs and segmentating in a strictly anterior to posterior manner during development, are primitive, e.g., Scoloplos, Haploscoloplos, etc., and including the Onychophora. For them the pelagic larvae of Tomopteris, Nereis, etc. are advanced. It should be noted that the egg of Arenicola cristata and Axiothella mucosa both contain much yolk, but A. cristata larvae possess a short free-swimming



Text-fig. 17: A, a late nauplius of Balanus (After Calman from Lankester, 1909); B, first nauplius larva of Cyclops fuscus (After Green from Barnes, 1962). anu, antennules; ant, antennae; md, mandibles; h, frontal horn; o, nauplius eye.

stage and are non-heteronomic, whereas A. mucosa has a heteronomic segmental process but is nonpelagic throughout life. In this light, the Anderson-Manton criteria for determining primitiveness among polychaetes are less than convincing (see also p. 125).

2. Ontogeny of Crustaceans

Crustaceans eggs are typical centrolecithal and cleavage is superficial; holoblastic cleavage is not uncommon. Often only the initial cleavage divisions are complete, as in some arachnides, but there are a considerable number of species of both Entomostraca and Malacostraca in which a hollow blastula is formed.

Since among the crustaceans the young hatch at different periods of development, the youngest larvae may have quite diverse forms in the various orders, representing different ontogenetic stages according to the degree of development they undergo within the egg. The earliest and basic type of crustacean larva is the nauplius (text-fig. 17). It is commonly free-swimming and planktonic, oval or pyriform in shape with the larger end anterior. Three pairs of appendages are present - the antennules, antennae, and mandibles - and a median eye of two or more parts, although there is no visible segmentation of the ectoderm;

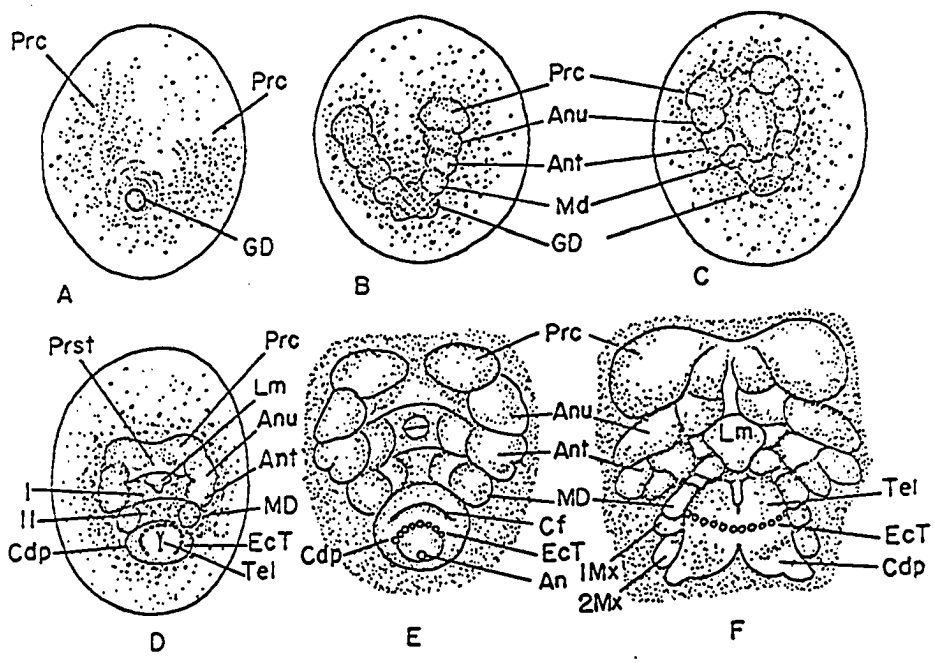
Text-fig. 17: A, a late nauplius of Balanus (After Calman from Lankester, 1909); B, first nauplius larva of Cyclops fuscus (After Green from Barnes, 1962). anu, antennules; ant, antennae; md, mandibles; h, frontal horn; o, nauplius eye.

---

the presence of appendages and ganglia shows that the nauplius is at least a partly segmented stage of development. The region of the body behind the mandibles is that in which the other segments will be formed later, and their rudiments may be seen beneath the nauplius cuticle. When these segments are formed, however, they are generated by a different method from that which formed the anterior segments. The nauplius is usually followed by a metanauplius stage, during which, in the course of successive molts, trunk segments, and additional appendages are gradually acquired from a subterminal zone of the nauplius; the posterior part of the body is much lengthened; it is now distinctly segmented and bears the rudiments of several pairs of new appendages.

Examples of Crustacean Ontogeny

a. The ontogenetic development of Leander squilla Linn has been studied by Sollaud (1923). The germ bands of Leander are at first V-shaped (text-fig. 18), its two arms diverge forward on the blastoderm from a posterior area of proliferation (GD) in the region of the blastopore, whence also are proliferated forward two corresponding bands of mesoderm. Each mesoderm band soon becomes divided into four consecutive parts, which appear as four lobes on the surface (B). The germ bands themselves gradually become less divergent, and finally their anterior ends curve medially and are united by a bridge between their anterior lobes (C). At the same time the rudiments of three pairs of appendages appear on the second, third, and fourth lobes, which are respectively the antennules (Anu), the antennae (Ant), and the madibles



Text-fig. 18: Early embryonic stage of a palaemonid crustacean. Showing the development of the procephalic lobes and the antennules from the unsegmentated prostomal region, and cephalic segmentation. A, Leander squilla Linn; B-F, L. serratus Pennant. Anu, antennules; Ant, antennae; Cdp, caudal papilla; Ect, ectodermal teloblasts; GD, germinal disk; I,II, primary somites; Lm, labrum; MD, mandible; 1Mx,2Mx, first and second maxillae; Prc, procephalic lobe; Prst, prostomium; Tel, telson. (After Sollaud, 1923 from Snodgrass, 1938.)

(md). The first lobes (Prc) have no appendages, but they give rise to the compound eyes and optic ganglia. These now appear in the ectoderm of the young embryo. Sollaud says that there are transverse grooves which appear before the first segmentation (D). The most anterior groove runs between the antennae and the mandibles, and the third behind the mandibles (D,E). The body of the embryo is thus divided into an anterior prostomial head segment (Prst), bearing the procephalic lobes and the antennules, a second segment (I) bearing the antennae, a third segment (II) bearing the mandibles, and a terminal unsegmented piece (Cdp), which is the caudal papilla. The embryo is now in the nauplius stage. Sollaud claims that the first segment, bearing the optic lobes and antennules, is the prostomium, the other two segments being the first and second true somites.

Text-fig. 18: Early embryonic stage of a palaemonid crustacean. Showing the development of the procephalic lobes and the antennules from the unsegmentated prostomal region, and cephalic segmentation. A, Leander squilla Linn; B-F, L. serratus Pennant. Anu, antennules; Ant, antennae; Cdp, caudal papilla; Ect, ectodermal teloblasts; GD, germinal disk; I,II, primary somites; Lm, labrum; MD, mandible; 1Mx,2Mx, first and second maxillae; Prc, procephalic lobe; Prst, prostomium; Tel, telson. (After Sollaud, 1923 from Snodgrass, 1938.)

The caudal papilla of the malacostracan embryo (text-fig. 18) projects from the blastoderm. In its distal part, there is a circle of

undifferentiated ectodermal (Ect) and mesodermal cells, which are the teloblasts that will generate the postnauplius somites. Beyond the teloblasts is the region of the telson (Tel) containing the anus (An). In its development the caudal papilla bends forward (F) beneath the part of the embryo contained in the blastoderm.

When the malacostracan embryo reaches the metanauplius stage there appear at the base of the caudal papilla the two maxillae and their appendages.

Sollaud (1923), however, asserts that in Leander both maxillary somites arise from the base of the caudal papilla before the beginning of activity in the teloblast, and that the first somite of the teloblastic series is that of the first maxillipeds. According to him the four somites of the metanauplius (F), namely, those of the second antennae, the mandibles, the maxillae, and the second maxillae, are primary somites formed directly in the primary embryonic body between the acronal prostomium and the caudal papilla. If so, the primary somites of the crustaceans would agree in number with the Xiphosurida and Trilobita. However, Snodgrass (1938, p. 81) thinks this interpretation is erroneous, since the maxillae are derived from the caudal papilla (see below).

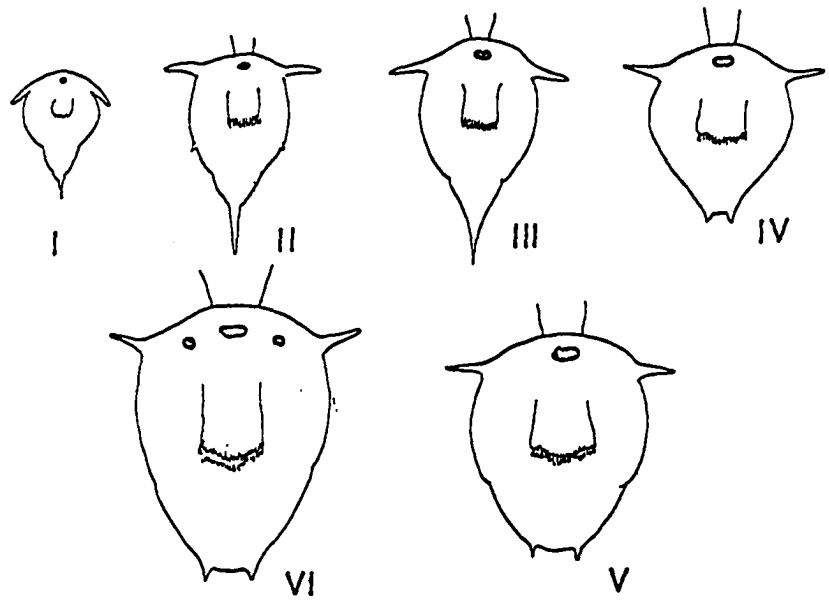
Manton's (1928, 1934) studies of the embryonic process of secondary segmentation of the crustaceans Heminysis and Nebalia agree with the observations of Sollaud for the embryo of Leander. In Heminysis, she says the nauplius and postnaupliar mesoderms are at first some distance apart, but later the teloblastic ectoderm and mesoderm extend forward to include the first maxillary segment. The teloblasts of Nebalia are

differentiated at the sides of the posterior blastoporic area, and the ectodermal teloblasts eventually form a complete circle around it; the mesodermal teloblasts are formed from the mesendodermal mass at the blastopore; Francemeier (1939) says they are proliferated from the ectodermal teloblasts. The ectodermal teloblasts, according to Manton, join the naupliar ectoderm between the mandiblar and first maxillary segments. Thus it seems that all segments between the mandiblar segment and the telson are formed by the teloblasts. Therefore, the maxillae represent secondary somites and the primary somites are restricted to the second antennae and mandibles only.

When the last abdominal segment is complete, the teloblasts disappear in both Hemimysis and Nebalia.

b. The ontogenetic development of Balanus amphitrate var denticulata Broch has been studied by Costlow and Bookhout (1958), who described six naupliar and one cyprid stages. In the naupliar stages 1 through 3 the carapace is about 0.15-0.25 mm. in length (sag.) and rounded to subrounded with a long terminal process. Two pairs of spines are marked along the margin of the carapace; the anterior lateral pairs are medium-short, and the posterior-lateral ones are rather small. Three pairs of appendages, antennules, antennae, and mandibles, bearing setules are directed laterally and lateral posteriorly; the abdominal process terminates in two short spines. The labrum is located on the anterior mid-central carapace (text-fig. 19, I-III).

In nauplius stage 4, the carapace is about 0.22 mm. in length without a terminal process, but a pair of short spines appear on the



Text-fig. 19: A growth sequence of Balanus amphitrite var. denticulata Broch. Showing the metamorphosis of the carapace. (After Costlow and Bookhout, 1958.)

posterior edge where the carapace is delimited from the caudal process. Six rows of minute bristles are found on the ventral surface of the abdominal process (text-fig. 19, IV).

In nauplius stage 5 and 6, the carapace is ovate and about 0.28-0.34 mm. in length (sag.). The anterior and posterior pair of spines of the carapace remain unchanged, except that the posterior ones are slightly more widely spaced than in the previous stage. The abdominal process bears six pair of bristles. A pair of eye spots develops beside the naupliar eye in the later stage (text-fig. 19, V, VI).

Cyprid stage. The rounded anterior end of the cyprid is the widest portion of the carapace which curves gradually to the posterior end. The degree of pigmentation varies considerably, but some brown pigment is always observed; when the bivalve carapace is closed, both the anterior and posterior ends are smooth.

It should be noted that the early ontogenetic development of Balanus is morphologically quite similar to some protaspides of trilobites, such as Cryptolithus, Tretaspis (Whittington, 1959, pl. 23, 26), and asaphids (Evitt, 1961, pl. 117), etc. Though this similarity may be interpreted as an adaptation to their presumed temporary pelagic life, since the trilobite larvae also represent an early stage of development, it may, on the other hand, be indicative of evolutionary affinities.

Text-fig. 19: A growth sequence of Balanus amphitrite var. denticulata Broch. Showing the metamorphosis of the carapace. (After Costlow and Bookhout, 1958)

---

3. Ontogeny of Merostomata (Xiphosura)

According to Shuster (1950, 1960), the eggs of the horse-shoe crab are laid between the tide marks on sandy beaches. A month or more later, hatching occurs and the smallest larvae average 4.5 mm. in length. These grow by stages, shedding their chitinous skin between each stage. After the first molt the larvae acquire a tail. In the first tailed stage their average length is 6.0 mm. and in the next six stages 9.55 mm., 14 mm., 21 mm., 29 mm., 40 mm., and 50 mm., respectively.

During the first few years of life the horse-shoe crabs shed their chitinous exoskeletons more than once a year, but when the animal attains a length from 100 to 120 mm. there is only one molt a year, and this occurs during mid-summer. Some nine to twelve years elapse before the horse-shoe crab is sexually mature. The sexual organs become functional and the accessory reproductive apparatus is developed with the final molt. Throughout the period of growth each horse-shoe crab molts 16 to 19 times; when a horse-shoe crab reaches the adult, sexually mature, stage, it seems to stop molting. However, occasional exceptionally large adults seem to contradict this.

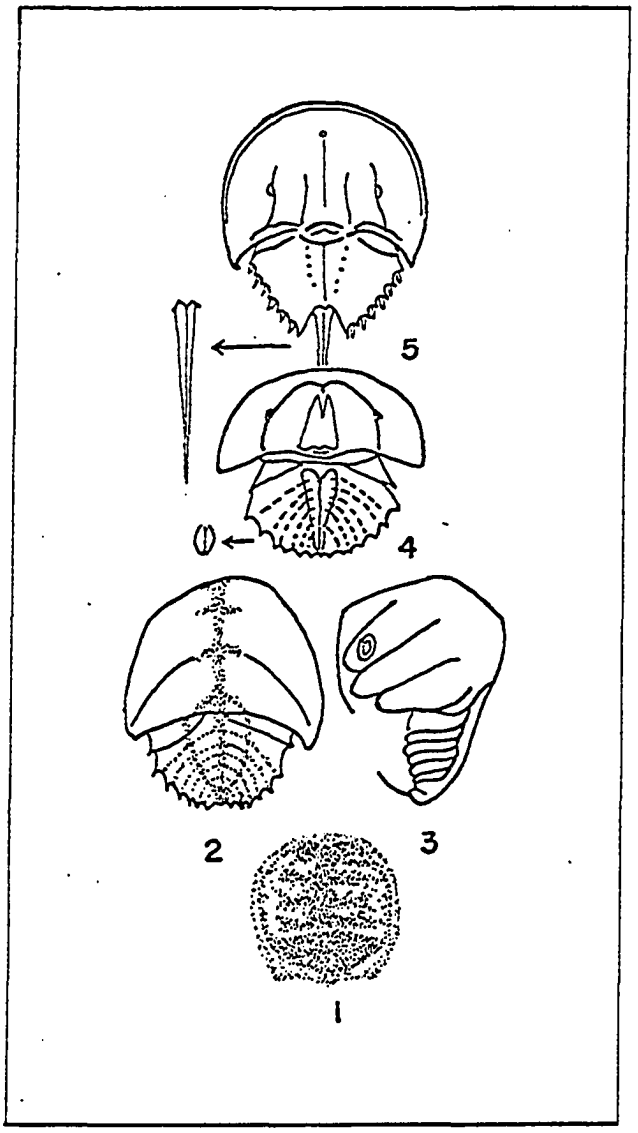
The opening of the exoskeleton during molt begins just within the ventral margin of the prosoma, the doublure. The first-tailed stage or smaller "horse-shoe crab" emerges within an hour, but an animal 100 mm. wide may require over 24 hours.

Measurements of the linear dimensions of the growing animal show that the increments of growth generally decrease during the life cycle after an initial increase. For example, the width of the first-tailed stage is 45% greater than that of the previous stage, 75% greater in

the next stage, but then decreases step-wise to a 15% increase in width in the twelfth stage.

Embryologic development of Xiphosura ("Limulus").- The earliest embryologic study of Xiphosura polyphemus was made by Milne Edwards (1838); the next classical studies of this subject were those of Lockwood (1870) and Packard (1972, 1880); all included detailed studies not only of embryology but also of ecology, anatomy, and histology. Packard strongly argued that the Trilobita and Merostomata are phylogenetically closely related, and he first recognized the "trilobite stage" of the early Xiphosura embryos. Kingsley (1885, 1892, 1893), in a series of papers, recognized 11 stages from egg to early hatching larva. Patten (1896, 1912) divided the early ontogeny of Xiphosura into 14 stages. Iwanoff (1933) studied the embryology of X. maluccanus ("Tachypleus gigas") and paid special attention to the development of the primary and secondary segments of the larval forms. According to him, the early larvae of X. maluccanus has four primary somites, which are the first to appear from the mesoderm, and are secondarily impressed upon the ectoderm. Thus demonstrating his phylogenetic principle. Størmer (1944) has followed Iwanoff's theory and separated the ontogenetic development of Xiphosura into four stages, namely, the trilobite, synziphosura, prestwichianella, and limulid stages. These growth stages apparently parallel the geological record and phylogenetic development of the animal.

In the earliest Xiphosura larva, the trilobite stage (Størmer, 1944) consists of four primary segments in front of the generative pygidium or caudal papilla. The secondary somites, or the new segments, are success-



Text-fig. 20: Ontogeny of a limulid.
1-4, Xiphosura maluccanus (Linn).
1, trilobite stage; 2,3, synziphorura stage; 4, prestwichianella stage; 5, limulid stage. (After Størmer, 1944.)

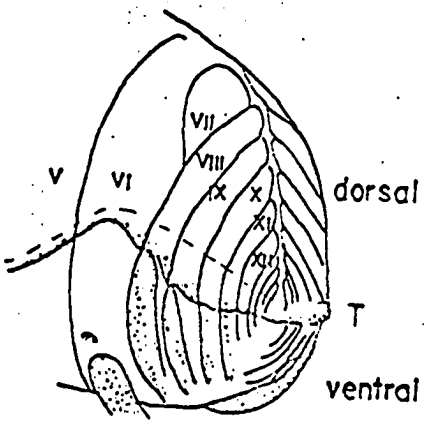
ively budded off from the pre-pygidial growth zone and serially added to the primary somites. The formation of the new segments is essentially the same as in annelids and crustaceans, but it seems that after the 6th cephalic, or 3rd secondary, somite are formed, the generative pygidium is turned forward, and comes to lie underneath the posterior margin of the cephalon, although Iwanoff failed to show this generative pygidial activity. This is an interesting parallel to the condition shown to occur in the ontogenetic development of the palaemonid crustacean Leander (text-fig. 18). Therefore as the result of this pygidial inversion, the 7th segment, or 3rd secondary somite, divides into two halves (7th and 8th) and a juncture forms between the prosoma with chilaria rudiments and the opisthosoma ridges (text-fig. 21). The same condition is seen in the occipital ring of olenellids and the cervical groove of crustaceans. Secondary segments are continuously added behind the prosoma to form the opisthosome; these are comparable to and perhaps

---

Text-fig. 20: Ontogeny of a limulid. 1-4, Xiphosura maluccanus (Linn). 1, trilobite stage; 2,3, synziphorura stage; 4, prestwichianella stage; 5, limulid stage. (After Størmer, 1944.)

---

homologous with the tertiary somites of trilobites (p.119). The opisthosomal segments are formed around the margin of the generative pygidium and arranged semi-concentrially at the early stage, but later open so as to arch forward and laterally (text-fig. 21, T). The adult structure of Xiphosura contains evidence of the presence of 14 post-oral

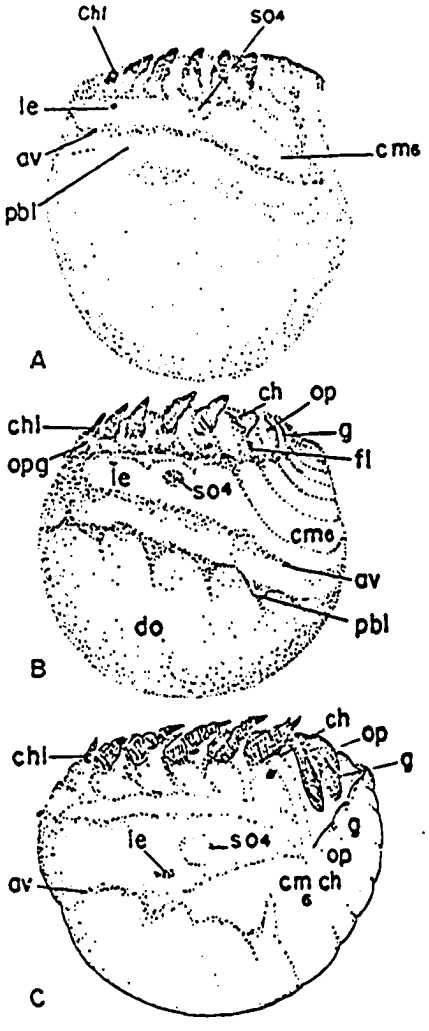


Text-fig. 21: Embryo of Xiphosura. Posterior-lateral view, showing the formation of secondary somites around the telson (T). (After Iwanoff 1933, from Störmer, 1942.)

somites, the last somite being behind the last gill-bearing segment; but Iwanoff says that in the embryo, rudiments of three somites appear in the post-branchial region, thus giving a total of 16 somites anterior to the caudal spine. The caudal spine of the xiphosurids is often called the "telson", but it is situated beyond the segment-forming zone. Therefore, Iwanoff suggests that it might be comparable with the dorsal spine on the posterior segments of certain Olenellus, where the spine arises from a segment some distance from the end of the body. Thus the xiphosuran "telson" may not be a true terminal structure, and several small somites beyond it may have been lost. This interpretation may be reasonable, but it should never be taken to mean that this condition has necessarily any phylogenetic significance, since many crustaceans and insects also possess a similar structure, which may be longer or shorter, slenderer or stouter, due to functional differences.

Text-fig. 21: Embryo of Xiphosura. Posterior-lateral view, showing the formation of secondary somites around the telson (T). (After Iwanoff, 1933, from Størmer, 1942.)

Patten (1912) has shown that the early limulid embryo has the lateral eyes situated on the anterior lateral margin of the shield. The eys migrate to a more doral medial positon during the later stage (text-fig. 22). Comparable migration of the eyes is also seen in opisthoparian and proparian trilobites. Moreover, the segmental sense



Text-fig. 22: Early embryos of Xiphosura polyphemus (Linn). A, showing segmental sense organ; note the forwardly located lateral eye and absence of any segmental furrow laterally on the prosomal region; B, the lateral eye has moved to the second segmental region; C, the abdominal lobe is distinctly marked off; the lateral eye has moved backward and dorsally to 4th cephalic segmental region.. av, anterior medial ventral margin of the cephalon; ch, cheliceral lobe; cm6, 6th cephalic segment; g, gill; fl, flabellum; le, lateral eyes; op, opercular segments; opg, optic ganglion; pbl, posterior dorsal plate; So4, 4th segmental sense organ. (After Patten, 1912.)

organ (text-fig. 22, So4), which appears in the early larvae of Xiphosura is comparable to and may correlate with the fixigenal node of certain immature trilobites (text-fig. 38H and 43E).

Text-fig. 22: Early embryos of Xiphosura polyphemus (Linn).
A, showing segmental sense organ; note the forwardly located lateral eye and absence of any segmental furrow laterally on the prosomal region; B, the lateral eye has moved to the second segmental region; C, the abdominal lobe is distinctly marked off; the lateral eye has moved backward and dorsally to 4th cephalic segmental region.
av, anterior median ventral margin of the cephalon; ch, cheliceral lobe; cm6, 6th cephalic segment; g, gill; fl, flabellum; le, lateral eyes; op, opercular segments; opg, optic ganglion; pbl, posterior dorsal plate; So4, 4th segmental sense organ. (After Patten, 1912.)

III. ONTOGENY OF TRILOBITA

The ontogeny of trilobites is divided into three different periods namely, protaspid, meraspid, and holaspid. Five stages of the periods are recognized: the protaspid period is subdivided into three stages: the anaprotaspid, metaprotaspid, and paraprotaspid; the meraspid period is subdivided into early and late meraspid stages; not stages of the holaspid (adult) period are recognized (text-fig. 23). Each stage presumably represent several instars (episodes of ecdysial moulting) during the succession of which the changes termed periods and stages of morphologic differentiation were attained. Nothing comparable to hexapod metamorphosis is here involved in the ontogeny. Thus the periods and stages are arbitrarily defined, since the morphologic changes of any trilobite during ontogeny were essentially gradual and continuous. Hypothetically, these morphologic changes have left no gap, no omission, except that conditions of preservation may cause a certain stage to be lacking in growth sequence. Neontologists have sometimes observed the pre-maturation of certain individuals within an ontogenetic assemblage, i.e., an immature specimen may be morphologically older than its age. If this phenomenon should occur among trilobites it would disrupt the regular growth sequence or lead to the misidentification of the growth stages, but since this situation is relatively uncommon in the Recent fauna, it would seem to present no grave problem in ancient ones.

1. Protaspid Period

Historical review. The term "protaspis" was first established by Beecher (1895, p. 169) for the earliest record of trilobite ontogeny, on the basis of features of the dorsal shield. He described it as: "minute, varying in observed species from 0.4 to 1.0 mm. in length, circular or avoid in form, axis distinct and more or less strongly annulated, head portion predomination, glabella with five annulations, abdominal portion usually less than one-third the whole length of the shield axis with from one to several annulations. Pleural portion smooth or grooved, eyes when present anterior, marginal or submarginal; free cheeks when present very narrow, marginal". This original concept of the protaspis now needs revision because we now know considerably smaller protaspides with only four or five axial annulations and for the most part lacking the abdominal part. Beecher (1895, p. 169) also suggested that "the protaspis period might be subdivided into anaprotaspid, metaprotaspid, and paraprotaspid stages during which the early and late molts took place, before the complete separation of pygidium or introduction of thoracic segments:. He did not give any distinctive characteristics to define these different stages. Raw's (1925, p. 226) view was that "the protaspid period embraces the various stages that precede the development of a definite transverse suture subdividing the dorsal shield". This definition clearly draws a line between the protaspid and the meraspid periods, and is now followed by most authors. Størmer (1942, p. 56) defined the protaspid period as "all the earliest stages from hatching to the appearance of the first transverse dividing of the dorsal shell into two separate shields, and the transitory pygidium".

Beecher 1895	Raw 1925 1927	Størmer 1942	Whittington 1959	Palmer 1958 1962	Hu 1968
	holaspid period	holaspid period	holaspid p.	holaspid p.	holaspid p.
	meraspid period n — 0	meraspid period n — 0	meraspid period n — 0	late meraspid stage	late meraspid stage
				m. meraspid stage	early meraspid st.
				e. meraspid stage	
paraprotaspid stage	protaspid period	metaprotaspid stage	protaspid < 0.6 mm	metaprotaspid stage	paraprotaspid stage
metaprotaspid "		anaprotaspid stage	0.4-0.5 "	anaprotaspid stage	metaprotaspid stage
anaprotaspid "			> 0.4 "		anaprotaspid stage

Text-fig. 23: Showing various author's divisions of the ontogenetic development of trilobites.

He also further defined the anaprotaspid stage as that in which "the axis has only five segments", and the metaprotaspid stage that which "includes the later stage in which new segments are added beyond those present in the anaprotaspis". Thus he was the first author to give a clear definition of Beecher's stages. However, the paraprotaspid

---

Text-fig. 23: Showing various author's divisions of the ontogenetic development of trilobites.

---

stage was not adopted. In Whittington's (1959b, p. 127) opinion, "the earliest protaspid represents the earliest stage at which, presumably, the exoskeleton is mineralized and therefore may be preserved. A range in length (sag.) from about 0.25-1.0 mm. is known, rarely larger. Outline in dorsal aspect is usually subcircular, convexity moderate to strong, and subspherical form may be attained. The axis is at least partially defined in the smallest protaspides...and may be completely outlined by furrows. From a length of 0.40 mm. upward it is in most specimens divided into rings, the anterior being longer (sag.) than those following it. The 5th...ring is the occipital, and behind this is the short axial portion of the protopygidium... The pleural regions of the smallest know protaspid ... are either incompletely divided or not at all. At a length of 0.50 to 0.60 mm. the transverse ridge (posterior border of cephalon) and furrow have either appeared or been completed, thus dividing the protaspis into a larger cephalic portion and smaller protopygidium...". I infer from this statement that he subdivided the protaspid period into three stages: the 1st stage being smaller than

0.40 mm., the 2nd stage between 0.40 to 0.50 mm., and the 3rd larger than 0.60 mm. (sag.); however, he did not denominate these three stages.

Palmer (1958, p. 165) followed Stǿrmer's definition, and divided the protaspid period into anaprotaspid and metaportaspid stages, and noted that "there is some evidence that the anaprotaspid axis may have more than five segments anterior to the occipital segment. Also some species, such as C. ["Cassifimbra"] walcotti (Resser) have an unsegmented axis in the protaspid. Nevertheless, the morphologic position of the posterior part of the occipital ring is nearly always apparent. The anaprotaspid stage might thus be less equivocally defined as the stage in which the dorsal exoskeleton is a shield showing no evidence of segmentation of a distinct protopygidium portion to the occipital ring". He recognized Stǿrmer's anaprotaspid and metaprotaspid stages as valid and identifiable subdivisions of the protaspid period for most non-olenellid and nonagnostid trilobites, but used a slightly different notation. The writer agrees with Palmer's statement that there are many trilobite larvae without any distinct axial annulation and distinct protopygidial separation. These are less easily categorized, but those forms with distinct annulation and protopygidium lend themselves well to the Beecher-Stǿrmer protaspid classification. The exceptional, and rarer, forms of protaspides are probably secondarily modified out of the common, and probably more primordial and general, undifferentiated condition (see p. 72). Palmer (1962, p. 92) also further subdivided the metaprotaspid stage into 4 degrees based on the distinct or indistinct separation and the number of the fixigenal

and pygidial spines; these subdivisions generally conform to Ross' (1951, p. 584) ontogenetic studies of Pseudocybele nasuta Ross. Such differences as exist are in minor details.

Thus it can be seen that, there is no complete agreement among trilobite students on the definition of ontogenetic stages; however, there is a consensus as to the reality of the protaspis stage and its divisibility despite the hazy and somewhat debatable boundaries of both stages and periods. It is obvious that the different interpreations of trilobite development are due to the study of different materials by the different researchers. The characteristics of all trilobite larvae are not all the same, and hence the different materials present somewhat different information, from which various generalized interpretations have been derived. The situation is very well demonstrated by modern crustacean larvae (p. 49) (as well as those of echinoderms, with variously different larval forms). It is now manifest that no single set of criteria can be used as the basis for the determination of ontogenetic stages of all trilobites. In this study an attempt has been made to find a comprehensive interpretation of all know trilobite ontogenies. In the search a certain body of new information has also accrued. Thus, the definition of period and stages used in this work is to some degree different from the definitions of most other workders. However these deviations are held to a minimum to lessen confusion.

A. Terms Used in this Paper

The protaspid period is the earliest known period in the ontogenetic development of a trilobite: the insters are generally 0.22-0.85 mm. in

length (sag.) and rounded to subrounded in outline. The shield may be gently to highly convex, with or without distinct axial and pleural lobe differentiations and axial annulation; such differentiation as does occur is fundamental. Surface ornamentation may be present or absent. The smallest instars usually have four axial rings and the largest ones well-developed cephalic and protopygidial shields. The anaprotaspid stage is the earliest subdivision of the protaspid period; the shield averages 0.28 mm. in length (sag.) and varies from 0.22 to 0.40 mm. long (sag.), with or without axial and pleural differentiations. The axial lobe is marked by four distinct or indistinct annulations. A longitudinal fissure may be present along the central axis, and well-preserved material may show one to three pairs of marginal spines, a spinose hypostoma, and the librigeno-rostrum underneath the shield. The metaprotaspid stage is the second subdivision of the proataspid period. The shield averages 0.35 mm. in length (sag.) and varies from 0.30-0.60 mm. (sag.). It may or may not show distinct differentiation of the axial and pleural lobes. Typically, the axial lobe is marked by 5 annulations; the longitudinal axial fissure of the prior stage may or may not show. Some silicified material shows one or more pairs of marginal spines, a sparsely spinose hypostoma, and undifferentiated librigeno-rostrum. The paraprotaspid stage is the third subdivision of the protaspid period. The average total length is about 0.58 mm. (sag.) and varies from 0.50-0.80 mm. (sag.). The shield is subspherical elongate and well-differentiated into cephalic and protopygidial shield by a definite transverse suture. The axial and pleural lobes are well differentiated, with or without axial annulation; the axial fissure may

show; facial sutures are dorsal or dorso-marginal; the librigeno-rostrum is separated; the number of hypostomal spines is fewer than in the preceding period. The protopygidium may be divided into a few segments by furrows, with or without marginal spines.

Palmer (1958, p. 165) pointed out that some protaspides have more than four glabellar segments, and Whittington (1959b, p. 134) stated that Shumardia larvae have three glabellar rings anterior to the occipital segment. It now appears that four glabellar segments is the general rule in protaspides: when more or less than four are present, it is probably due to secondary segmentation of the frontal lobe or segmental fusion. Such "segments" should not be considered as truly initial segments.

B. Representative Types of Protaspides

Agnostids

The ontogeny of agnostids commonly is neglected in discussions of trilobite larval development, and our knowledge of the ontogeny of this group has not advanced much since Barrande's (1852) period. The youngest known form has a cephalon and a pygidial shield. The thoracic segments are subsequently added serially between them. Matthew (1896) distinguished three ontogenetical stages of this group based on the characteristics of the pygidium: the early larval, the later larval, and the adult stages. Šnajde (1957) described the ontogeny of several species of agnostids but none of the morphologic structures shown pertain to stages earlier than those represented in Barrande's studies. Hunt (1967, p. 203-208) reported on the development of Trinodus elspethi (Raymond)

but his silicified material from the Edinburg Formation of Virginia shows no earlier growth stage than was previously known. If there was a protaspid, the stage earlier than the two shield one, it is still unknown.

The present study of Pagetia clytia Walcott is the first report on the ontogeny of the eodiscinid group. The earliest instar shows a large cephalic shield and somewhat smaller pygidial shield without any distinct suture between [pl. 1, fig. 23]; well-elevated posterior fixigenal borders are aresent. The total length of the shield is less than 0.30 mm. (sag.). The axial lobe is cyclindrically conical, with three indistinct annulations. Judging from the indistinct separation of the cephalic and pygidial shields, and from the size, this specimen belongs to the paraprotaspid stage or between paraprotaspid and early meraspid stages.

Olenellids

The first ontogenetic work on the olenellids was by Ford (1877) who studied the ontogeny of Elliptocephala asaphoides Emmons from the Lower Cambrian of New York. Walcott (1910) studied the same form from the Lower Cambrian of Alberta and Paedeumias yorkense Resser and Howell from the Lower Cambrian of Pennsylvania. The ontogeny of Paedeumias hanseni Poulsen was described by Poulsen (1932) from the Lower Cambrian of Greenland, and Holmia kjerulfi (linnarson) by Størmer (1942) from the Lower Cambrian of Norway. Most of these ontogenies were reinvestigated by Whittington (1957a, 1957b, 1959b). According to him none of the supposed protaspides of olenellids truly belong to the protaspid period, since the specimens are all too large for the protaspis stage and all

have well-developed thoracic segments, a characteristic of later stages.

Palmer (1957) recently described a few silicified specimens from the Lower Cambrian of Nevada. He recognized five different growth stages, designated by Roman numerals I-V, but none of the specimens was judged as protaspid by Palmer or by Whittington (1959b) who reviewed the work.

A few very small shields or cephala of Olenellus truemani Walcott from the Lower Cambrian of Mexico were examined during the present study. They are about 0.40-0.55 mm. in length (sag.), spherical to subspherical in outline and convex, with well differentiated axial and pleural lobes. The axial lobe is marked by a longitudinal fissure, and the pleural lobes bear well impressed pleural furrows. Possibly there is a small protopygidium located behind the occipital ring [pl. 2, fig. 1-5]. If a small protopygidium is present behind the occipital ring, it is safe to assign the specimens to the paraprotaspid stage. The Mexican early larvae are different from those of published Olenellus or related genera in that the axis is fusiform and marked with a longitudinal fissure; the pleural lobes bear distinct segmental furrows, and the occipital ring is very narrow (sag.).

In discussing these specimens with Dr. Whittington at Harvard University in 1966, he suggested that they possibly belong to protaspides. There seems to be no doubt that these specimens are the earliest instars of olenellids yet seen.

Ptychopariids

The ontogeny of ptychopariids is better known than for any other trilobites. The classical foundations were laid down by Barrande (1852),

who figured and described a considerable number of larval stages including those of Sao hirsuts Barrande and Hydrocephalus carens Barrande, which are well known from illustration in paleontology text-books. Brögger (1875) described a larval series of Liostracus linnarssoni Brögger from the Middle Cambrian of Norway. Beecher (1895) reviewed these studies and was the first to make a comprehensive study of the ontogenetic development of trilobites and therefrom attempted a natural classification of the Trilobita. Strand (1927) and Størmer (1942) demonstrated the eye-ridges and cephalic segments of the early larvae of Olenus gibbosus (Wahlenberg). Endo (1935) worked on the ontogeny of Blackwelderia kobayashii Endo, Kobayahsi and Kato (1951) and presented detailed illustrations of the growth sequence of Redlichia chinensis Walcott. Recently, Palmer (1958, 1962) and Whittington (1941b, 1956e, 1959a, etc.), both working on silicified materials of Cambrian and Middle Ordovician ages, contributed much new information on the ontogeny and ventral morphology of early ptychopariid larvae. Whittington (1959b) also reinvestigated many of the old ontogenetic works, restudied original specimens, and has given a very complete summary of the ontogenetic development of trilobites.

The material here studied consists both of silicified and calcified forms. The typical protaspis of the ptychopaiids is a rounded to subrounded, convex shield; the total length of the instars is about 0.22-0.80 mm. (sag.); most of the shields are differentiated into axial and pleural lobes, but undifferentiated forms are common; the axis is either annulated or smooth, often marked with a longitudinal fissure along the axis; a pair of pits occur on the anterior lateral margin of

the shield; the under-side of the shield shows a complete librigena-rostrum of one plate and a spinose hypostoma. The librigenae are well-developed in the later stages and occur in front of the first pair of marginal spines. The protopygidium is marked by a few segmental furrows during the later stage.

The anaprotaspis varies from 0.22 to 0.28 mm. in length (sag.); the axis is composed of four annulations of varying distinctness, which are usually divided by a longitudinal fissure along the central axis and separated by transverse ring-furrows; the librigeno-rostrum is a single plate; the hypostoma is spinose. The typical examples of this stage have been studied for: Dytrmacephalus granulosus Palmer [p.237, pl. 9, fig. 1], Flexicalymene granulosa (Foerste) [p.312, pl. 19, figs. 1-4], Welleraspis lata Howell (Hu, 1964, p. 96, pl. 24, fig. 19), and Crepicephalus deadwoodiensis, n. sp. [p.218, pl. 8, figs. 1,2].

In the metaprotaspid stage the shield is 0.30-0.45 mm. in length; the axis is composed of five annulations of varying distinctness and the axial and pleural lobes are well differentiated. Some forms may present a narrow fringe along the posterior margin of the shield, but not segmented; the librigeno-rostrum is one unit; the hypostoma has a smaller number of marginal spines than the earlier stage. Examples of this stage have been examined in: Dunberbergia ? anyta Hall and Winfield [p.228, pl. 9, fig. 2-6], Ptychaspis bullasus Lochman and Hu [p.246, pl. 11, fig. 1], Olenus gibbosus (Wahlenberg) [p.253, pl. 12, fig. 1-3], Ptarmigania aurita Resser [p.181, pl. 4, figs. 6,7], and those of genera described in the anaprotaspid stage.

In the paraprotaspid stage, the shield is subrounded and elongate

with well differentiated cephalon and protopygidium; the dorsal furrows are distinct to indistinct; in most of the forms the longitudinal fissure has disappeared; secondary pits appear on the anterior lobe; the facial sutures are dorso-marginal and the palpebral lobes are well defined. The protopygidium is transverse or triangular, with or without marginal spines. The librigenae and rostrom are distinctly separated, and the marginal spines of the hypostoma are reduced. The dorsal furrow and the annulations of most genera show varying shallowness. Examples of this stage have been examined for: Apomodocia conica, n. sp. [p.204, pl. 3, figs. 4-8], Gylyphaspis cf. parkensis Rasetti [p.190, pl. 5, figs. 6,7], Cedarina cordilleae (Howell and Duncan) [p.211, pl. 7, figs. 5-8], Missisquoia cyclochila n. sp. [p.282, pl. 14, figs. 4-7], Libertella corona, n. sp. [pl. 16, figs. 1-4, 7, 8], and for those genera indicated in the previous stages.

Asaphids

The ontogenetic studies of asaphids have not progressed as far as those of ptychopariids. Ross (1951b, p. 579) studied a complete silicified growth series of Menoparia genalunata Ross, from the Lower Ordovician of northeastern Utah. The early instars of this form show the shield strongly enrolled, and the librigenae situated between the anterior and the posterior pair of spines. Whittington (1959a) studied the ontogeny of Remopleurides and Robergilla and showed that the larval forms are similar to those of Meoparia genalunata. All have a pair of posterior fixigenal spines, with the librigenae developed in between them along the lateral margin of the cranidium. Evitt (1961, p. 986-995)

established an excellent growth series of Isotelus? which showed again the small instars with a pair of anterior and posterior cranidial spines. Both Whittington's and Evitt's specimens were collected from the Middle Ordovician of Virginia.

Leptoplastus salteri (Callaway) (Raw, 1925, 1927) and Norwoodella halli Resser (Hu, 1963) possibly belong to this group since both show a development similar to that of Isotelus. The larvae of Leptoplastus have the librigenae located between the anterior and posterior fixigenal spines, and those of Norwoodella have the protopygidium developed before the cephalic and pygidial shields are differentiated. The early librigenal structures of both genera are unknown.

The protaspis of this group is spherical to subspherical in outline, convex, and about 0.25-1.00 mm. long (sag.); the surface is roundly smooth with a finely impressed dorsal furrow and anterior pits. The librigeno-rostrum is undivided in the earlier larvae but separated in the larger forms. The large palpebral lobe occurs between the anterior and posterior cranidial horns. The hypostoma is relatively large and spiny. The unity of the shield is characteristic; the protopygidium is well developed before the cephalic and pygidial shields differentiated; it thus seems that the pygidial and cephalic shield developed as a single plate without a distinct suture between them. This marks them as different from the protaspis of ptychopariids where the protopygidium is consistently sutured to the cranidial shield; moreover, the asaphid distinctness is pointed up by the fact that their librigenae occur between the anterior and posterior pairs of crandial horns, and most of the shields are without distinct axial and pleural lobal differentiation.

In the anaprotaspid stage the convex shield is rounded or ovate and ranges from 0.25 to 0.35 mm. in length; the axial and pleural lobes are not differentiated except for a longitudinal fissure along the central axis; the anterior pits are distinctly impressed. The silicified specimens show a pair of anterior and posterior shield spines, an undifferentiated librigeno-rostrum, and a spinose hypostoma. During the present study this stage was established for Isotelus stegops Green [p.330, pl. 20, fig. 17]; possibly Evitt's (1961, p. 988, pl. 117, fig. 1-4, and text-fig. 1) asaphid represents this stage, and also Hu's (1963, p. 130, pl. 19, fig. 18-24) study of Norwoodella halli Resser.

In the metaprotaspid stage the shield is rounded to subrounded, convex, and varies from 0.35-0.45 mm. in length (sag.); the axial and pleural lobes are separated by faint dorsal furrows. The longitudinal fissure may be present or absent; the librigeno-rostrum is a single plate and ankylosed with hypostoma. Evitt (1961) has stated that the librigeno-rostrum and hypostoma are separated at this stage; this may be questionable since these structures are evidently undifferentiated in ptychopariids of the same stage (see pl. 9, figs. 3, 6), and none of the material examined which seems referable to this stage shows librigeno-rostral-hypostomal sutures. It is unfortunate the shale material which has been studied here of Isotelus stegops Green [p.330, pl. 20, fig. 18, 19] fails to preserve these parts. An Asaphid illustrated by Evitt (1961, p. 988, pl. 117, fig. 5-9 and text-fig. 2) and Norwoodella halli Resser (Hu, 1963, p. 130, pl. 19, fig. 16, 17) are possibly representatives of this stage.

In the paraprotaspid stage the shield is elongate and subrounded

with the axial and pleural lobes well differentiated. The shield ranges from 0.50-1.00 mm. in length (sag.); it lacks a distinct posterior cephalic border and all signs of shield separation; the protopygidium occurs at the posterior margin of the shield; the dorso-lateral facial suture is located between the anterior and posterior cranidial horns. For Isotelus stegops Green [p.330, pl. 20, fig. 20,21] and probably for some other asaphis, (e.g., Evitt, 1961, pl. 117, fig. 9-19, and text-fig. 3,4) the earlier metaprotaspides are now known. Some of the early instars of Menocaria genalunata Ross (Ross, 1951, p. 577, pl. 81, fig. 1-9), Norwoodella halli Resser (Hu, 1963, p. 131, pl. 19, fig. 11-15), and Whittington's (1959a, p. 397) protaspides of Remopleurides possibly belong to this stage.

Phacopids and Trinucleids

There are few ontogenetic studies of phacopids and trinuclids, and most have revealed incomplete suites. No early protaspis is known. The classical ontogenetic studies of this group are those of Barrande (1852) on Dalmanitina socialis (Barrande) and Onnia ornata (Sternberg), both from the Ordovician of Bohemia. Some additional material of Dalmanitina socialis was studied by Whittington (1956a). All of the specimens of D. socialis and O. ornata show well developed pygidium. Their total length from the anterior border to the posterior pygidial margin is about 1.0 mm. (sag.). The ontogeny of Triarthrus eatoni Hall from the Utica Shale (Upper Ordovician) of New York State which is possibly a member of this group, was studied by Walcott (1879) and recently re-examined by Whittington (1957); the smallest known form has

both cephalic and protopygidial shield well preserved and may include one or two thoracic segments. Poulsen (1923) published a growth sequence of Peltura scarabaeoides (Wahlenberg), and the original specimens were likewise re-examined by Whittington (1958); the smallest form shows five glabellar annulations and a pair of broadly open posterior marginal spines, possibly with a small protopygidium between them. Temple (1952) studied the ontogeny of Dalmanitina olini Temple from Scandinavia and North Wales. He did not separate the protaspides into stages, but comparison of the size and morphologic structures of the shield shows that the smallest ones are early paraprotaspides. Whittington (1956a) re-examined Beecher's (1893) supposed odontopleurid protaspis, which belongs actually to a Phacops; this specimen also bears a well developed protopygidium, which indicates that it is a late protaspis. Størmer (1930) described the ontogenetic development of the Norwegian trinucleid, and assigned the smallest forms to "degree 0" of the early meraspid period, and none of the specimens could be judged as protaspides.

The growth stages of two genera which belong to this group were reviewed during the present investigation: Calliops strasburgensis Ulrich and Delo and Cryptolithus bellulus (Ulrich). All bear a well differentiated protopygidium, which indicates that they had developed at least beyond the metaprotaspid stage.

Generally, the smallest instars of this group are very similar to those of ptychopariids, except that the librigeno-rostrum remains unseparated throughout life. Three different groups of the larval form are recognizable; all belong to the paraprotaspid stage. 1), In the first group, the shield bears an anteriorly expanded glabella, spinose

surface, and small pygidial shield, such as Dalmanitina socialis (Barrande) (Barrande, 1852, pl. 26, fig. 1-3; Whittington, 1956a, p. 106, pl. 24, fig. 6,7,10), Dalmanitina olini Temple (1952, pl. 9, fig. 1-3 and pl. 10, fig. 6), and undetermined phacopid (Whittington, 1956a, p. 105, pl. 24, fig. 1-5), Calliops strasburgensis Ulrich and Delo [p.304, pl. 18, fig. 1,2]. 2), In the second group the shield is distinctly separated into cephalic and pygidial shields of almost equal size; the cephalic shield bears punctured fixigenae and a small median eye tubercle. This group includes Onnia ornata (Sternberg) (Barrande, 1852, pl. 30, fig. 41,42) and Cryptolithus bellulus (Ulrich) [p.320, pl. 20, fig. 1]. 3), In the third group, the shield bears a fusiform glabella, with distinct axial ring furrows and finely granulose surface. This group is represented by Shumartia pusilla (Sars) (Whittington, 1959b, p. 129, fig. 87A), Peltura scarabaeoides (Wahlenberg) (Whittington, 1958, p. 200-206, pl. 38, fig. 1-7), and Acerocare ecorne Angelin [p.260, pl. 13, fig. 1,2].

2. Meraspid Period (Traditional)

The second division of trilobite growth sequence is the Meraspid period. The term was proposed by Raw (1925, 1927), who defined it as follows: "later a suture comes to separate the cephalon from the post-cephalic rudiment, or 'transitory pygidium' of Barrande, and between these the free throacic segments.... are later, in effect, interpolated one by one, till the thorax is complete". Following Barrande (1852), he further divided the meraspid period into "degrees:, marked by the addition of new segments to the thorax, and numbered them from 0 to N

according to the number of segments in the thorax. These ontogenetic divisions are followed by most authors, but his degrees are difficult to recognize because most of the fossils are compressed, distorted, or disassociated. Hence, the degrees of the meraspid period for such material cannot be ascertained. Furthermore, those having the same number of thoracic segments in different species may not be in the same degree of development, since different trilobite genera or species vary in the same number of thoracic segments. For example, the "degree 8" in Paedeumia yorkense Resser and Howell and the same "degree" of Isotelus stegops Green are not at the same age level, the "degree 8" for the P. yorkense is juvenile, whereas for I. stegops it is an adult. The pygidium of I. stegops consists of about 12 segments, whereas that of P. yorkense is of one only; therefore, I. stegops at "degree 8" has 20 segments (8 thoracic segments and 12 pygidial ones) and is an adult, while P. yorkense at the same degree has 9 segments only (8 thoracic segments and possibly one pygidial segment) and is juvenile. The "degree" system can be useful only for marking the stages of an individual species. This being true, the term "degree" loses its meaning, since we are looking for terms which uniformly represent the ontogenetic stages common to all trilobites. Raw's definition of the mereapid seems valid. It can be subdivided on the basis of arbitrary criteria into early meraspid and late meraspid stages without any "degrees". This means that whereas Raw's "degree" subdivisions represent the absolute ages of the instars of an individual species, the subdivisions here employed pertain to all trilobites, and are comparable.

Kobayashi (1951, p. 112) proposed two meraspid terms based on the condition of the facial suture: anameraspid, i.e., without facial suture, and metameraspid, i.e., with facial sture. These terms have not been adopted by any other authors. Palmer (1958, 1961) uses early, middle, and late meraspid stages, instead of "degree". This system has much to recommend it. However, here in only early and late meraspid stages designations made because it seems better in keeping with the practice in neontology, and makes fossil and Recent ontogenetic data better comparable. Thus, trilobite ontogeny is here considered to be divisible into three periods: protaspid, meraspid, and holaspid. The protaspid period is subdivided into three stages, the meraspid into two, and the holaspid or adult is undivided. In the protaspid period the trilobite larva underwent rapid morpholic change, in the meraspid period there was slow change, and in the holaspid very little or none (text-fig. 25).

2A. Meraspid Period (Reconsidered)

The meraspid period is the second division in the ontogenetic development of trilobites. The cephalon is about 0.40 to 1.20 mm. in length (sag.), rounded to subrounded in outline, and low to high in convexity; the glabella of the early meraspid forms is divided into rings by distinct or indistinct transverse furrows; and become more deeply impressed during the later stages; the anterior brim first appears; palpebral lobes and ridges are well defined; the dorso-facial suture cuts the crandium into a trapezoidal to subtrapezoidal shape; free thoracic segments and definite pygidium are present. Commonly the

instars of this period were disassociated after the molt; the librigenae, thoracic segments and pygidium being scattered. Therefore, if an isolated immature cranidium is found, it is quite likely to belong to the meraspid period.

In the early meraspid stage, the cephalon averages 0.50 mm. in length (sag.) and bears transverse glabellar furrows of varying definition. A narrow anterior border appears along the anterior glabellar margin; the palpebral lobe is located in front of the mid-line of the glabella (tr.). The late meraspid stage, the cranidium averages about 0.70 mm. in length (sag.), and is trapezoidal in outline; the glabellar furrows are completed, and the preglabellar field appears between the anterior border and the anterior glabellar margin. The palpebral lobes are located near to or on the mid-line of the glabella (tr.).

2B. Types of Meraspides

Agnostids

The cephalon of agnostid meraspides varies from 0.25-1.4 mm. in length (sag.); the thoracic segments, which are added between the cephalic and pygidial shields, vary from none to two or three. In the early meraspid stage of the agnostids the cephalon is about 0.25-0.60 mm. in length; the thoracic appears with one segment; the pygidial axis is conical or subrounded, e.g., Kormagnostus simplex Resser [p.157, pl. 1, fig. 1, 6-8]. In the eodiscids, the cephalon averages 0.40 mm. in length (sag.) and bears a slenderly conical glabella and narrow anterior border. The glabella bears a frontal lobe, two axial rings and an

occipital one. The best examples of this stage are known for Pagetia clytia Walcott [p.162 pl. 1, fig. 15-17, 24, 25].

In the late meraspid stage the cephalon is about 0.50-1.20 mm. in length (sag.) with a broad anterior and broad conical glabella (eodiscid); the pygidial axis is subquadrate or rounded, with more than one thoracic segment (agnostid). This stage is described from instars of Pagetia clytia Walcott [p.163, pl. 1, fig. 18,19,26,27] and Komagnostus simplex Resser [p.157 pl. 1, fig. 2,4,9,10,12-14].

Barrande (1852) divided the agnostids into five developmental degrees (1-5) from early to adult forms. Whittington (1959b) adopted Raw's "degree" terms but interpreted specimens through the range from no thoracic segments to those with two thoracic segments as pertaining to meraspid degree 0 to 1. This possibly correlates with Barrande's "degrees" 1 to 4. Here the early meraspid stages of K. simplex Resser and P. clytia Walcott would correspond to Barrande's degrees 1 to 3, and those of the late meraspid stage to degree 4.

Olenellids

The meraspid period of olenellids is characterized by a rounded shield with broad anterior brim, a cylindrical glabella, narrow crescentic palpebral lobes, and a shield length of about 0.60 to 1.90 mm. (sag.). This period differs from the previous one in having no longitudinal fissure along the central axis, a narrower glabella and the fixigenal spines appearing laterally.

In the early meraspid stage the shield is 0.70 to 1.30 mm. in length, roundly conves, without a preglabellar field; the palpebral

lobe and the cephalic segmental furrows are distinct. Examples studied are Olenellus truemani Walcott [p.169, pl. 2, fig. 6-10,20,23] and Laudonia canadiensis, n. sp. [p.175, pl. 3, fig. 20,21].

This stage corresponds to Palmer's (1957) stage I to III of the ontogenetic development of Olenellus gilberti Meek and of Paedeumias clarki Resser and possibly to Walcott's (1910) early larvae of Paedeumias yorkense Howell and Resser (Walcott, 1910, pl. 32, fig. 2; Whittington, 1959b, fig. 96A).

In the late meraspid stage the shield varies from 1.42 to 2.0 mm. in length (sag.) with a narrow preglabellar field and shorter and broader palpebral lobe; the genal spine appears at the posterior lateral shield margin. The species in which this stage has been studied are: Olenellus truemani Walcott [p.170, pl. 2, fig. 11-14,21] and Laudonia canadiensis, n. sp. [p.176, pl. 3, fig. 25,28,29]. This stage is equivalent to Palmer's (1957) stages IV to V of Olenellus gilberti Meek, Störmer's (1942, pl. 2, fig. 6,7 and text-fig. 5e) young larva of Holmia kjerulfi (linnarsson), Whittington's (1957a, p. 935, pl. 115, fig, 1-3) Elliptocephala asaphides Emmons and to Paedeumias yorkense Howell and Resser of Walcott (1910, pl. 1, fig. 3-8), and to Paedeumias yorkense Howell and Resser of Whittington (1959b, fig. B and C).

Ptychopariids

The cephalon of the ptychopariid meraspid period bears well developed dorsal facial sutures; the cranidium is trapezoidal or subtrapezoidal in outline and varies from 0.60 to 1.60 mm. in length (sag.), rarely extending from 0.40 to 1.80 mm.; the glabella may or may not bear

distinct glabellar furrows; the anterior border appears earlier than the preglabellar field. The pygidial segments are ankylosed and frequently associated with small number of free thoracic segments.

This is the largest group within trilobites, and most of the ontogenetic studies which have been done belong to this group. The immature forms differ from those of olenellids by their smaller palperbral lobe, dorsal facial suture, and shields which lack a horse-shoe-shaped marginal border; but these characteristics are not always distinct and intermediate conditions occur, for example, in Redlichia, Paradoxides, Hydrocephalus, etc.

In the early meraspid stage the crandium is trapezoidal or sub-trapezoidal in outline, and about 0.60-0.95 mm. in length (sag.); the glabellar furrows distinctly or indistinctly cross the axis; the anterior border appears along the anterior glabellar margin; the protopygidial segments are not in a definite form and commonly associated with more than one free thoracic segment. This statement accurately describes certain of the early meraspid larvae but the stage features are more ambiguous. For example, in Dunderbergia ? anyta (Hall and Whitfield) [p.230, pl. 9, fig. 13,14,27,28,33], Dytremacephalus granulosus Palmer [p.239, pl. 10, fig. 15,17,24,29,30,32], and Olenus gibbosus (Wahlenberg) [p.254, pl. 12, fig. 9-12], the cranidia bear distinct glabellar furrows and hence the age is easily distinguishable, while Apomodocia conica, n. gen. et sp. [p.204, pl. 3, fig. 9-16], Glyphaspis cf. parkensis Rasetti [p.191, pl. 6, fig. 1,2,10,11], Crepicephalus deadwoodiensis, n. sp. [p.220, pl. 18, fig. 11-13,21] and Cedarina cordillerae (Howell and Duncan) [p.212, pl. 7, fig. 9,10,26] all lack distinct glabellar furrows. There-

fore, it is difficult to know their precise ontogenetic position; but since all of these latter forms, within the appropriate size range, lack a preglabellar field, it appears that they are also early meraspides.

This illustrates the need for less rigidly approaching the stage-dating of trilobite larvae. A broader spectrum of traits than is customarily employed for this purpose has much to recommend it.

In the late meraspid stage the cranidium ranges from 0.90-1.60 mm. in length (sag.) and is subtrapezoidal to trapezoidal in outline; the glabellar furrows are all complete; the preglabellar field generally appears; the pygidial segments are ankylosed and take on the specific configuration. They are articulated with several thoracic segments. The best examples are presented by several genera as noted in the previous stage. Here again, no limited set of characteristics will serve the whole group for stage recognition. For example, Ptarmigania aurita Resser [p.183, pl. 4, fig. 19,20] and Ptychaspis bullasus Lochman and Hu [p.148, pl. 11, fig. 8-13,26,27,31] lack a preglabellar field, but comparison of the position of the palpebral lobe, the width of the fixigena, and the differentiation of the glabellar furrows with that of the earlier stage, make stage assignment reasonably secure.

As noted previously, Palmer (1958, 1962) divided the meraspid period into three stages: early, middle or intermediate, and later meraspid stages. The middle merspid of Palmer correlate with the early meraspis here; the late meraspis are the same; but his early meraspid stage is equivalent to the paraprotaspid or represents between the paraprotaspid and early meraspid stages are here differentiated (text-fig. 23).

Asaphids

The cranidium of the meraspid period of asaphids is characterized by well-differentiated axial and fixigenal lobes; the dorsal and glabellar furrows are distinct or indistinct; the palpebral lobes are large and situated at the mid-length of the glabella; the silicified material shows the early forms with a pair of large anterior and posterior cranidial spines, but these spines have disappeared in the larger, later ones; the posterior fixigena is very narrow. The pygidium is rounded to elongate, with or without posterior marginal spines.

In the early meraspid stage, the crandium is quadrate in outline except for a pair of large anterior horns; the anterior border appears; the palpebral lobe is situated between the anterior and posterior fixigenae. The pygidium bears posterior marginal spine. The asaphid species in which this stage has been observed are Menoparia genulunata Ross (Ross, 1951b, p. 579, pl. 81, fig. 10-13 and 1953, p. 634, pl. 62, fig. 6,7,9,10,13,16), and Remopleurides, meraspides degree 0, (Whittington, 1959a, p. 398), and possibly degrees 1-4 or 5 of Leptoplastus salteri (Callaway), (Raw, 1925, 1927), and the early meraspid stage of Norwoodella halli Resser (Hu, 1963, p. 131, pl. 19, fig. 5-10).

In the late meraspid stage the subquadrate cranidium varies from 1.50 to 2.50 mm. in length and lacks anterior horns; the anterior border and preglabellar field appear. The palpebral lobe is smaller than in the previous stage. The pygidium lacks marginal spines. Instars belonging to this stage are described for Isotelus stegops Green [p.33/, pl. 21, fig. 14,15,22-24,27], Isotelus ? (Evitt, 1961, p. 99, pl. 117,

fig. 20-23), Monocaria genulunata Ross and/or Scinocephalus solitecti Ross (1951b, p. 581, pl. 81, fig. 14-19), and larger meraspid cranidia of Whittington (1959a, p. 399). Questionable members of this stage are Raw's (1925) degrees 5 or 6 to 12 of Leptoplastus salteri (Callaway) and Norwoodella halli Resser (Hu, 1963, p. 131, pl. 19, fig. 3-4).

It should be pointed out that the early protaspides of Isotelus ? of Evitt (1961) and the late protaspides of Remopleurides of Whittington (1959a) are possibly a continuous growth sequence of the same species and genus; this interpretation is based on both the size of the skeletons and morphologic characters; for example, the largest protaspis of Isotelus is about 1.0 mm. long with a rudimentary protopygidium and an indistinctly developed posterior fixigenal border; the smallest meraspis of Remopleurides is about 1.3 to 1.5 mm. in length (sag.) with well developed protopygidium, posterior fixiegenal border, and dorsal furrows; both show continuous morphologic and size variation. Furthermore, both genera came from the same locality and were presumably etched out from the same material, the Remopleurides lacking early protaspides and the Isotelus? lacking early meraspides. Hence, these larvae could belong to the same growth sequence, or if they really belong to the two genera indicated, then these genera must be phylogenetially closely related. Unfortunately, the ontogenetic evidence of Isotelus stegops in the Cincinnati materials is no better than Evitt's, and does not help to resolve the problem.

Phacopids and Trinucleids

The ontogenetic information on phacopids and trinucleids is mostly

incomplete, both in the published data and the present material. The only significant morphologic differences from the ptychopariids is the presence of an undivided librigeno-rostrum. Otherwise the description of ptychopariid meraspides serves here, at least until fuller data are discovered. However, there are three distinct types of development: Dalmanitid, Trinuleid, and Triarthrid.

Dalmanitid. The cranidium is occupied by a forward-expanded glabella and lacks an anterior border; the palpebral lobe varies from small to large and extends from the anterior lateral margin of the cranidium back to the posterior fixigenal border. Examples include Calliops strasburgensis Ulrich and Delo [p.304, pl. 18, fig. 3-13], Dalmanitina socialis (Barrande) (Barrande, 1852, pl. 26, fig. 4-11), and Dalmanitina olina Temple (1952, pl. 9, fig. 4-6, and pl. 10, fig. 1-5).

Trinucleid. The instars all have distinctly separated cephalic and pygidial shields; the cranidium is transverse, semicircular; the fringe increase in width and the eye-ridge decreases in length during growth. Examples include Cryptolithus bellulus (Ulrich) [p.32, pl. 20, fig. 2-8, 11], Onnia ornata (Sternberg) (Barrande, 1852, pl. 30, fig. 43-50 ?), and Reedolithus carinatus (Ang) (Størmer, 1930, p. 34, pl. 4, fig. 2-4, pl. 5, fig. 1-3).

Triarthrid. The early meraspides all have incomplete glabellar furrows, and a narrow anterior border appears along the preglabellar margin. In the late meraspides, the glabellar furrows are well-separated, and a narrow preglabellar field appears. Types of this group are Triarthrus eatoni (Hall) (Whittington, 1957, p. 941, pl. 116, fig. 1-9), Peltura scarabaeoides (Wahlenberg) (Whittington, 1958, pl. 38, fig. 8-18),

and Acercoare ecorne Angelin [p.260, pl. 13, fig. 9-12,20,22,26], and possibly Shumardia pusilla (Sars) (Whittington, 1959, p. 129, fig. 87B-G).

3. Holaspid Period

The holaspid period is the last period of the trilobite life history. The term was introduced by Raw (1925, p. 226): "the Holaspid period covers the development after the completion of the thoracic", and also (1927, p. 16) "the Holaspid period...is that of the greatest growth in size, accompanied by a more modern development of form". Stubblefield (1936, p. 351) drew attention to the literal meaning of "Holaspis" - complete shield - and suggested that it should be applied only to trilobites in which complete post-cephalic segmentation has been attained. Raw's definition is adopted here. During the holaspid period only minor differentiation takes place and the specific characteristics are achieved. Such changes transpire as increase in size, the shortening of lengthening of spines, deepening or shallowing of the furrows, widening or narrowing of the border, etc. These changes progress slowly and are complete only after a long period of time, and many molts.

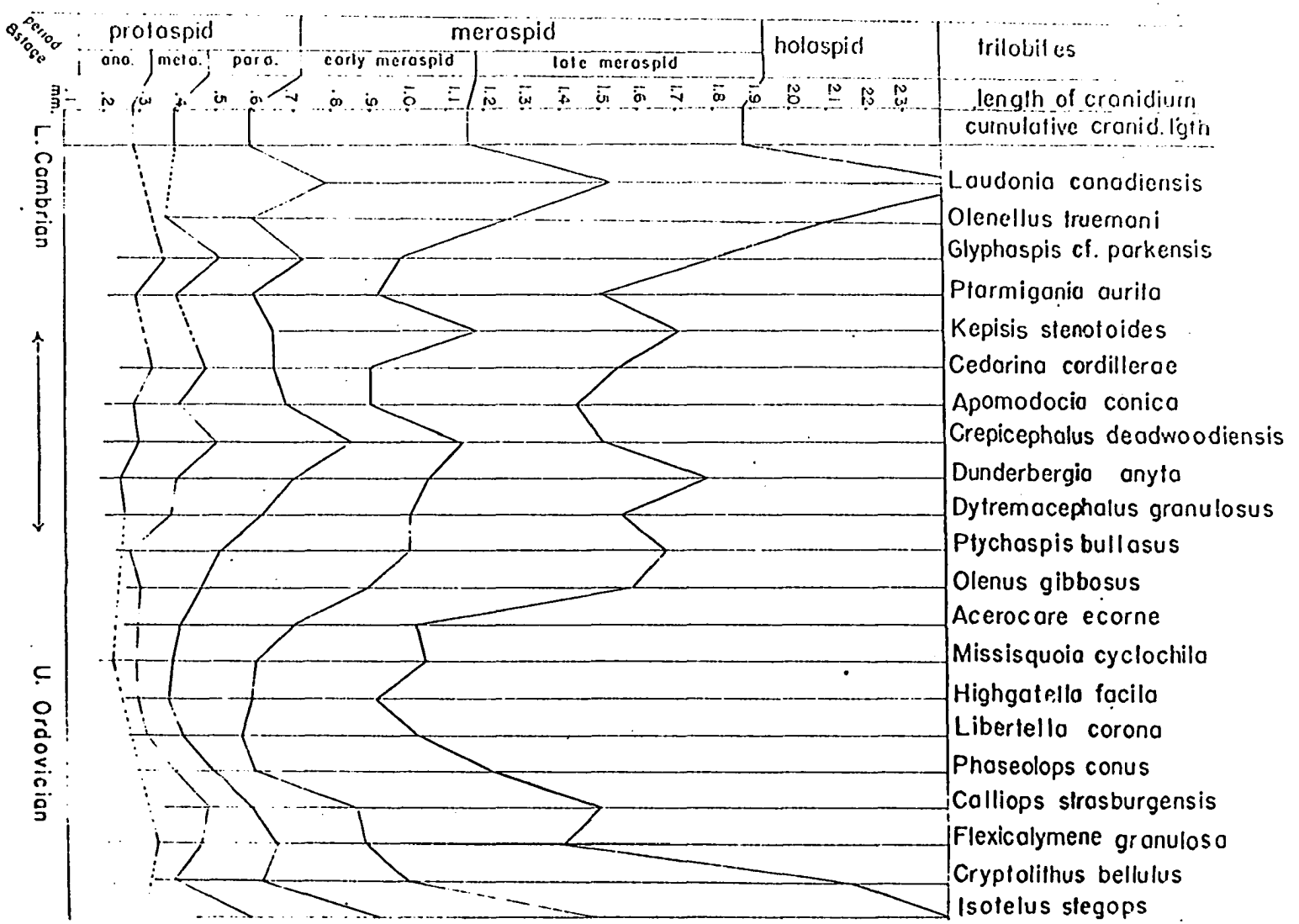
4. Rates of Growth in Trilobites

The skeleton of trilobites covered the dorsal surface of the animal and extended a variable distance under the ventral surface as the doublure. The organic material was strengthened by mineral secretions, probably, mainly of calcium carbonate, but seemingly also of calcium phosphate. Preservation is extremely variable. The exoskeleton may be complete, but far more often it occurs as dissociated parts. The

complete skeleton of many species is unknown, and almost no trace of soft parts is preserved. There was undoubtedly also a delicate ventral integument but it too is unknown. From a few localities have come specimens preserving the appendages. These complete or dissociated exoskeletons may be preserved in virtually any kind of marine sediment. In fine-grained sediments the skeletons, though flattened, are sometimes only partly, or not all, disarticulated. In both muddy and relatively pure limestone the exoskeletons are usually not flattened or distorted, though commonly disarticulated. In recent years Whittington, Palmer, Ross, Hintze, and Robison have also recorded beautifully and delicately preserved silicified specimens of both adults and larvae from limestone dissolved in glacial or hydrochloric acid. These materials add greatly to knowledge of trilobite morphology.

A. Variation in Larval Size

The Early Cambrian olenellid larvae, which have been found by many paleontologists, are all recognized as late protoaspides or early meraspides, and the most immature larvae of the later Cambrian are mostly younger in ontogeny. This phenomenon could be interpreted as being due to the rate of mineralization of the animal skeletons. A statistical study has shown that the rate of the skeletal mineralization has increased during geologic time (text-fig. 24). Early Cambrian trilobites have mostly large sized larvae which are preserved only in the later developmental stage, whereas the later Cambrian larvae are smaller and are of early ontogenetic stages. This feature could reflect the relatively unmineralized condition of the exoskeleton of early Cambrian



Text-fig. 24: Graph showing the rate of growth of trilobites and their size distribution through the Cambrian and Ordovician.

Text-fig. 24: Graph showing the rate of growth of trilobites and their size distribution through the Cambrian and Ordovician.

trilobites, such as olenellids. Possibly their early protaspides were not yet mineralized, therefore, no fossils remain; whereas the protaspides of late Cambrian or geologic younger trilobites, such as ptychopariids had mineralized skeletons. This assumption also correlates with the increase in thickness of the trilobite skeleton: geologically earlier forms have thinner skeletons than later forms. Walcott (1918, p. 176) pointed out that "all known trilobites had a more or less chitinous shield or carapace which was thick and strong in the Illaenidae etc., or thin and delicate in the Mesonacidae, Olenellus etc.". When olenellid trilobite skeletons have been compacted together or two individuals interplicated, then the features of the lower individuals are always impressed upon the upper one during the compaction following deposition (Howell and Resser, 1938, p. 207, pl. 12, fig. 2). This bespeaks the yielding nature of the integument in the early forms.

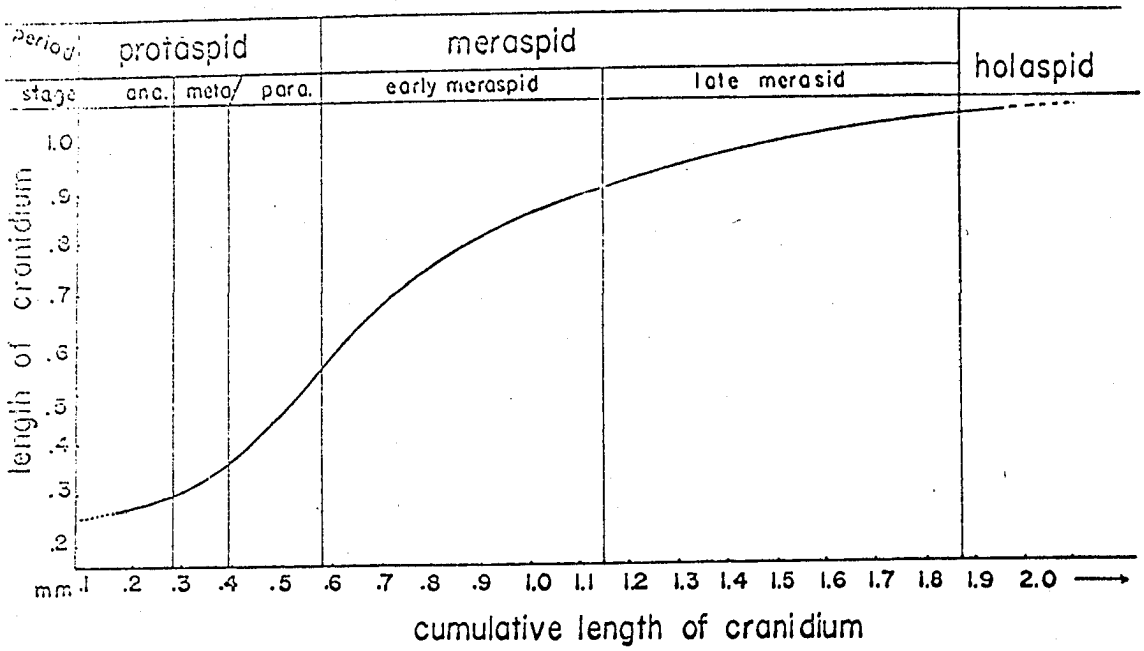
The size of protaspides is not contstant. Stǿrmer (1942, p. 94) noted that "the size of the protaspid seems largely to correspond to the size of the adult". It appears that the protaspid instars average about 0.28 mm. in length (sag.). Extremely small instars may be as small as 0.22 mm., such as those of Ptarmigania, Cedarina, and Dunderbergia, etc.; the largest ones are more than 0.80 mm. in length (sag.), as in Olenellus, Glyphaspis, Crepicephalus, Isotelus, etc. The geologically early larvae are larger than those of later epochs. It is interesting, however, to note that the late Ordovician early larval forms, such as Calliops, Flexicalymene, Isotelus, etc., are very much like those of the early Cambrian with large larvae. Their protaspids average about 0.45 mm. (sag.). Thus it would seem that a generalization with respect to the

gradual decrease in size of early instars through time is unacceptable. In the meraspid period, the cranidium averages about 0.90 mm. in length (sag.), the extreme forms may extend from 0.40 to 2.3 mm. long (sag.). Missisquoia, Highgatella, and Acerocare are the smallest, and Olenellus Kepisis, Crypotolithus, and Isotelus are the largest.

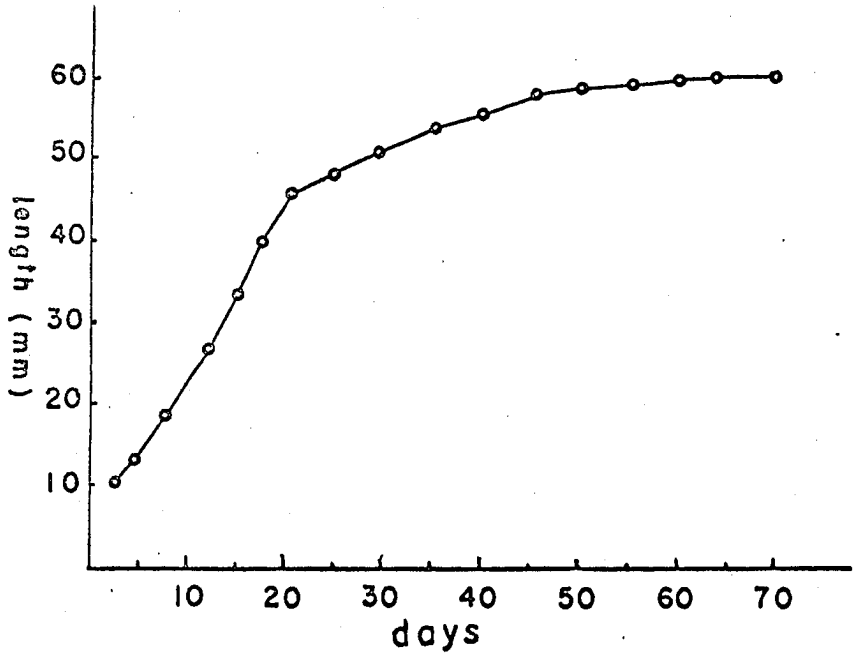
B. Growth-rate Correlated with Instar Periods

Protaspid period. During the anaprotaspid and metaprotaspid stages, the shield undergoes distinct changes in its marphologic characters; the most significant is the addition of the new axial segment; whereas the earliest stage has only four, the later instars develop five; the axial rings and the longitudinal fissure may disappear, but little increase in length. During the paraprotaspid stage, the cephalon has five axial rings and a protaspid pygidium is added posterior to the cephalon. In this stage the length may increase more than twice that of the earliest stage (text-fig. 25).

Meraspid period. The early meraspid is the great developmental stage of a trilobite as it involves the differentiation and growth of cranidial structures. The glabella grows longer than that of the protaspis; the anterior and posterior cranidial borders are defined. The cranidium shows about a four-fold increase in length from the average sized protaspis to the end of the early meraspid period. During the late meraspid stage, the cranidium develops a preglabellar field and distinct glabellar furrows, but the rate of the increase of glabellar length is very much less than in the early meraspid stage; the cranidium is about five times longer than the average sized protaspis



Text-fig. 25: Showing the cranidial growth-rate at different ontogenetic stages of trilobites. Notice that the length of the cranidium increases rapidly during the paraprotaspid and early meraspid stages. (Data based on text-fig. 24.)



Text-fig. 25a: Growth curve of crustacean Daphnia magna, reared in the laboratory. Note that the cuve shows general configuration of the curve resembles that of trilobites (text-fig. 25). (After Green, 1961.)

and about one-fourth longer than that of the early meraspid stage. The growth rate is greatly reduced during this stage, in comparison with the protaspis and early meraspid stages.

Text-fig. 25: Showing the cranidial growth-rate at different ontogenetic stages of trilobites. Notice that the length of the cranidium increases rapidly during the paraprotaspid and early meraspid stages. (Data based on text-fig. 24.)

Raw (1927, p. 15) reported that Leptoplastus salteri increased six-fold during the me raspid period (between his degrees 1 and 12) and Sao hirsuta ten times during the meraspid period. Westergård (1936) calculated that Paradoxides pinus ? Holm increased 17-fold. Stubblefield (1926) showed that Shumardia pusilla increased seven times. Whittington (1957, p. 434) assumed that "during the meraspid period the length of the trilobite increased to some 6 to 14 times that of the largest meraspis...". It should be pointed out that the rate of cephalic increases may not correspond to the increases of the thorax. The rate of increase of cephalon and thorax are unequal. The thorax increases in length far faster than the cephalon, since the thoracic segments are added mainly during meraspid period.

The increase in rate of body growth possibly indicated that the animals underwent rapid adaptation. It is reasonable to assume that as the pelagic larvae of trilobites changes their mode of life to the benthonic or borrowing habitat, the rate of growth should increase in

order to adapt to the new environment. Hupé (1953, p. 3-5, fig. 1,2 and 1954, p. 43-44, fig. 28) has pointed out that the more steeply rising growth curves seem to characterize the geologically younger trilobites.

The variation of growth rate corresponding to the age of the individual is also seen in other taxa, the best example that has been given is that of Xiphosura ("Limulus") (p. 57) and Green (1961, p. 66-67) [text-fig.25a] studied on the growth of Crustacea.

5. Cephalic Segmentation

Study of the segmentation of trilobites has to depend on external structure only, for nothing of the internal structures are known except for muscular markings on the inside of the skeleton which are occasionally preserved. Commonly, in the modern arthropod the "head" is a complex structure consisting of a large procephalon with a few forwardly migrated body segments joined to it to form a cephalon. This phenomenon has been demonstrated by embryologists and antomists, but for trilobites this characteristic is inferential and the number of cephalic segments is difficult to determine.

In the late 19th centruy Bernard (1894), who studied adult trilobites, considered the trilobite cephalon to be composed of five segments, of which four segments were supposed to lie behind the laterally projected and posteriorly curved first segment. Beecher (1895), from his ontogenetic studies of trilobite carapaces, pointed out that the early larval instars had an axis apparently composed of five segments. Walcott (1910, p. 237) identified seven segments in the trilobite cephalon: 1, an anterior border segment; 2, an ocular segment; 3, a palpebral or first glabellar segment; 4-6, the second to fourth

glabellar segments; and 7, the occipital segment. In a later paper, Walcott (1918, p. 126) omitted the anterior border segment, thus postulating a trilobite cephalon composed of six segments. Raw (1927, 1937, p. 375, etc.) in his several papers believed that the glabella originally included six segments as supposedly shown in several meraspid larvae and certain adult forms. Størmer (1942) studied the ontogenetic development of Olenus gibbosus and noted that the earliest known larvae or "anaprotaspis" stage has five primary segments. He tried to correlate these five segments with the primary segments of the Xiphosura embryo. Subsequently, Raw (1953), Hupe (1953), and Palmer (1957), from their morphologic and ontogenetic studies of olenellids, considered the head to be composed of a minimum of eight primary dorsal segments.

The earliest protaspis or anaprotaspis found in the course of this study is about 0.22 mm. in length (sag.) with four segments. This has been observed in Dunderbergia ? anyta Hall and Whitfield [p.227, pl. 9, fig. 1], Dytremacephalus granulosus Palmer [p.237, pl. 10, fig. 1], Missisquoia cyclochila, n. sp. [pl. 14, fig. 1], Flexicalymene granulosa (Foerste) [p.312, pl. 19, fig. 1-4], Welleraspis lata Howell (Hu, 1964, p.96, pl. 24, fig. 19). All of the specimens show either a small or a large procephalon (frontal lobe) and three post-oral segments. The pleural segmental furrows, while commonly not distinct, are in some speciments clearly seen.

A. Primary segments

The segments of the trilobite body from the anterior margin of the cephalon to the posterior end of the pygidium are differentiated into

three regions; the primary, secondary, and tertiary segmental regions. The primary segmental region, or archicephalic region, includes a procephalon and two post-oral segments; the secondary segmental region consists of the third and fourth axial segments, i.e., the preoccipital and occipital segment. The tertiary segmental region consists of the thoracic and pygidial segments.

Procephalon. The earliest instar of the trilobite consists of four cephalic segments; the procephalon, two post-oral, or primary, segments, and a small terminal portion, or the generative disc. The procephalon is the extreme anterior portion of the trilobite head, or archicephalon. It is located anteriorly to the preoral region, and is composed of hypostoma, rostrum, antennules, librigenae, eyes, preglabellar field, and the first glabellar segment. The procephalon is delimited by the posterior branch of the facial suture, palpebral ridges, and dorsally by the first pair of glabellar furrows. This portion is probably homologous with the acron or prostomium of polychaetes, which is not segmented, but superficially divided into a few plates (p. 43-44).

The hypostoma is the extreme anterior portion of the procephalon. It is separated from the rostrum or librigeno-rostrum by the rostral suture. This plate, of variable size and shape, lies underneath the anterior-central portion of the cephalon. The early hypostoma is proportionally considerably larger in relation to the body than in late growth stage. The early hypostoma often bears a spinose margin and small, longitudinal median body. This condition is well shown in Olenellus truemani [p.167, pl. 2, fig. 20], Dunderbergia ? anyta [p.229,

pl. 9, fig. 28,29], and by an asaphid described by Evitt (1961, pl. 9, fig. 5-39). The marginal spines are reduced during the later growth stages while the median body increase in size during ontogeny. The surface of the hypostoma varies from smooth to granulose, ridged, or maculate.

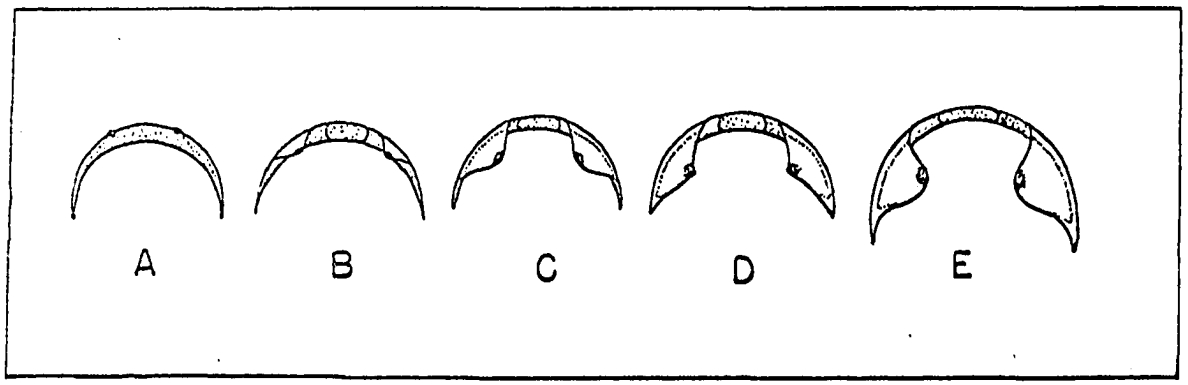
The maculae, when present, (and in many trilobites this portion of the hypostoma is preserved), are located on the central lateral sides of the hypostoma or slightly anterior to this. The maculae commonly show a surface pattern of granules, regularly or irregularly disposed, or are roughly reticulated or rather regularly facetted [pl. 20, fig. 26]. Lindström (1901, p. 35-70) has published a comprehensive study of these structures, and concluded that the maculae are true ventral visual organs. This interpretation is favored by Hupé (1953), whereas Raymond (1920), Størmer (1949), and Whittington and Evitt (1953) regard them as places of muscle attachment. An alternative suggestion is that these structure reflect the position of the statocyst sacs which are seen in many curstaceans, polychaetes, scyphozoans, etc. In the crustaceans the statocysts are restricted to a few groups of Malacostreca, where only a single pair are present and are diversely located, in the base of the antennules, on the base of the abdomen, uropods, or telson. Each statocyst arises as an ectodermal invagination and is unusally expressed on the exterior. The statolith may be a tissue-secreted structure, but commonly is composed of a mass of agglutinated sand grains. The physiology of crustacean statocysts is best known in the decapods (shrimp, crayfish, lobsters, and crabs).

Statocysts of various kinds are also found in certain polychaetes:

in several species of Arenicola, in several ariciids, in Loimia and Lanica among terebellids, and in sabellids. All of these are burrowers or tube-dwellers in which orientation may be very important. Apart from the ariciids, which may have several pairs of statocysts, a single pair is most commonly found, unusually situated in one of the most anterior segments. There is no doubt that these are all gravity perceptors. Removal or destruction of the statocysts causes the animal to lose its orientation. The nuchal organ of the polychaete, which is located on the frontal lobe of the acron, may also have the same function as statocysts. This nuchal organ is another candidate for possible correlation with the maculae of trilobites.

No detailed examination of this problem has been made, but considering the location of the maculae, their presence or absence on diverse hypostomata, as well as their different morphologic features, this interpretation should be reasonable. If maculae are statocystic, their study may help very much in reconstructing the mode of life of trilobites, and help to relate them to the habits of modern animals: burrowing, benthonic or pelagic. The so called "panderian organ" may also have had the same function as statocysts.

Librigeno-rostrum. This plate, of various sizes and shapes, is located underneath the anterior-ventral margin of the cephalon or rotated onto the dorsal surface to form various types of librigenae. Ontogenetically, the librigena, perrostrum or rostrum are homologous. The librigeno-rostrum may be separated into three parts (a pair of librigenae and a rostrum) or two parts (a pair of librigenae only) or without any separation (text-fig. 26). In the ptychopariids the



Text-fig. 26: Showing the ontogenetic development of the librigenae and the migration of the eyes of trilobites. Schematic.

librigeno-rostrum is separated into three parts by connective sutures. In the asaphids it is separated into two parts by a median suture, and the olenellids and phacopids are without any separation. Hence the undivided perrostrum may be the original condition and the two or three-part condition derived (see p.150).

Jaekel (1911), Hupé (1951, p. 473), and Raw (1953, p. 114) named the librigeno-rostrum the "ocular segment". Morphologically, the ocular segment is synonymous with the librigeno-rostrum, but ontogenetically it is doubtful if this part is an independent segment. It seems rather to be a part of the acron or procephalon which became separated by secondary segmentation to facilitate molting.

Text-fig. 26: Showing the ontogenetic development of the librigenae and the migration of the eyes of trilobites. Schematic.

The eyes are situated on the librigenae, as most authors believe (Jaekel, 1901; Warburg, 1925; Herrickson, 1926; Størmer, 1942; and Hupe (1951). Beecher (1897) pointed out that during the earliest larval stage, the lateral eyes migrate from the margin or submargin towards their median position in the adult. This observation is supported by the development of most ptychoparids and a similar migration is also seen in the development of Xiphosura (p. 62 and text-figure 22). However, there are exceptions. In some forms the eyes are initially located dorsally of supermarginally, e.g., in olenellids, trinucleids and harpids (pl. 2, and 20). Therefore, it seems safer to allocate the eyes simply to the procephalon or acron, and to recognize that

several modes of ontogenetic ocular shift occur among trilobites.

The frontal lobe is the first glabellar segment, and is probably homologous with the posterior portion of the acron of the polychaete. In the early ontogenetic stages this segment is generally larger than in succeeding stages, e.g., Ptarmigania aurita (pl. 4), Glyphaspis cf. parkensis (pl. 5), and Calliops strasburgensis (pl. 18) etc.. However, this condition does not always prevail; Crepicephalus deadwoodiensis (pl. 9), Ptychaspis bullasus (pl. 11), Acerocare ecorne (pl. 13), and Flexicalymene granulosa (pl. 19, fig. 1-4) among others, show a first first glabellar segment which in initially relatively smaller than in later instars. The frontal lobe shows varying degrees of separation by glabellar furrows. During later development the frontal lobe may become expanded or reduced in size. Størmer (1942, p. 117) believed that "the strong development of the frontal lobe is apparently dependent on the more powerful development of the alimentary canal, which probably extended forward from the mouth in a fold below the glabella, just as in "Limulus". If the procephalon of trilobites is homologous with the acron of polychates, then the frontal lobe, whether small or large, of the early protaspis may be representative of the corresponding brain-case, since we now know that the longitudinal fissure which characterizes the early protaspid axis disappears during the later growth stages. The disappearance of the longitudinal furrow may reflect expansion of the alimentary canal. This metamorphosis of the axial lobe may indicate that the alimentary canal was not located directly underneath the frontal lobe.

Anterior pits. A pair of pits of varying definition is located at

the sides of the first glabellar segment or frontal lobe. These pits generally appear very early on the anterior margin of the protaspid shield, and become shallower and indistinct later. In early ontogeny the pits are mostly rounded to oval but become elongate or linear during the later stages. The pits are poorly developed among the olenellids, agnostids during early stages but are rather well-impressed later (pl. 2, fig. 16-18; pl. 1, fig. 4,5). Generally, with these exceptions, the anterior pits are distinctly marked in the early larval stage and become shallow later on. Ptarmigania aurita (pl. 4, fig. 1-23), Glyphaspis cf. parkensis (pl. 5, fig. 1-15), and Acerocare ecorne (pl. 13, fig. 1-13) are good examples.

The anterior pits were thought to be attachment for antennules or muscles by Beecher (1895, p. 179) and Størmer (1942, p. 116). Whittington (1941, and 1953, p. 50), who studied both silicified and calcified materials of Flexicalymene senaria (Conrad) and F. meeki (Foerste), found that the pits correspond to the anterior lateral wing processes of the hypostoma. His view was that "the development of anterior pits and corresponding wing processes on the anterior wings of the hypostoma is interpreted as a mechanism for support (cranidium) but not articulation of the hypostoma". This was a significant discovery.

Palpebral ridges. The palpebral ridge is a raised strip connecting the proximal side of the eye and the axial furrow behind the anterior lateral corners of the first glabellar segment. In the early ontogenetic stages the ridges are indistinct; they presumably curve forward from the antero-lateral margin of the shield to extend behind the anterior pits (pl. 8, fig. 5,7; pl. 11, fig. 2), but they are generally not recognizable

until the later stages. These ridges sometimes appear in the immature stages but disappear during later immature stages, or perhaps early holaspis, as in Cryptolithus bellulus (pl. 20, fig. 1-6). In some forms such as Isotellus stegops (pl. 20, fig. 17-30) the ridges are always indistinct and another asaphid described by Evitt (1961, pl. 117, fig. 1-23). In the olenellids the ridges are unknown.

The palpebral ridges also appear on the cephalon of agnostids (pl. 1, fig. 5) where they curve forwardly from the anterior pits to the anterior-lateral margin.

The palpebral ridges may lie along the line of ankylosis of the procephalon and the post-oral segmental tips. An interesting comparison can be made with the formation of the prototroch of the trochpore larva, due to forward migration of the peristomium.

Cephalic sutures. There is on the head of trilobites a single major cephalic suture delimiting the cranidium from the librigeno-rostrum. It presumably reflects a major cleavage during moulting. Various names have been applied to this suture as a whole (e.g., grand suture) or for diverse courses that it pursues: perrostral, opisthoparian, proparian, hypoparian, gonatoparian suture, etc.. Some of these courses have been employed in the past as major taxobases.

Beecher (1895, p. 117-178) was of the opinion that the librigena had a ventral position in the early stages and migrated toward the margin and backward over the cephalon to the adult position. This interpretation has been validated by subsequent ontogenetic studies of silicified trilobites. Since the librigena originated in a ventral position and migrated onto the dorsal surface during the later growth

stages, the grand suture or its derivitives accompanied the migration of the librigeno-rostrum onto the dorsal surface. The submarginal position of the facial suture is primordial in all trilobites; from this location various patterns are derived (pl. 9, fig. 3,6,11,27; pl. 10, fig. 3,9,29). From the perrostral or hypoparian sutural types, the opisthoparian, proparian, and grand suture plans are developed.

Hupé (1953) presented supposed evidence of the existence of a dorsal or metaparian suture in the olenellid trilobites, where previously no facial suture had been observed. He suggested that the dorsal suture was present and open in ancestral olenellids but became closed during later evolution. Vestiges of the supposed dorsal sutures are seen on some of his specimens from the Lower Cambrian. His illustration (1952, pl. 1-5) shows two ridges on the preglabellar field and a pair on the posterior lateral fixigenal areas. However, the ridges (pl. 1, fig. 3,5, etc.) on the preglabellar field may not be suture but impressions of the perrostrum. Most of the Lower Cambrian trilobites had thin exoskeletons, as was pointed out earlier (p. 97). Some of Hupé's illustrations (pl. 1, fig. 1,3,6) show a well preserved and undisturbed perrostrum. The coincidence of the limits of the perrostrum and the preglabellar "sutures" make one suspicious of Hupe's conclusion. Moreover, the posterior fixigenal ridges, which show in his photographs, appear not to be a facial suture ankylosis but rather the preoccipital segment ankylosis. The existance of this suture as described by Hupé was denied by Størmer (1942, p. 141) who says "I find no direct evidence of the anterior and posterior eye-line representing trace of a facial suture in the Olenellidae". Moreover, uncompacted calcareous specimens show no

preglabellar field ridges or lines such as those seen in Hupe's shaly specimens, and the posterior lateral fixigenal ridges are well marked [pl. 2, fig. 14-19; pl. 3, fig. 28-31]. It seems that Hupe's hypothesis is untenable, no facial sutures are recorded on the dorsal surface of the olenellid dephalon.

B. Post-oral Segments

The post-oral segments include the 2nd to 4th glabellar and occipital segments, i.e., two primary and two secondary segments. The secondary segments are derived from the generative disc. These segments are possibly homologous with the antennae, madibles, and maxillae 1 and 2 of crustaceans. The segmental furrow may be distinctly or indistinctly marked; the pleural furrows are shown on Olenellus truemani (pl. 2, fig. 1-10) and are less impressed on Olenus gibbosus (pl. 12, fig. 4,6), Dytremacephalus granulosus (pl. 10, fig. 4,5) and others.

The pleural segmental furrows were first demonstrated by Størmer (1942) from his ontogenetic study of Olenus gibbosus. Whittington (1957, p. 467) reinvestigated Størmer's original material and came to the conclusion that the pleural segmental furrow is hypothetical. Whittington's views are in turn subject to review, for, unfortunately, most ptychopariid instars do not show the well impressed pleural furrows as clearly as olenellids do. In Olenus gibbosus and Dytremacephalus granulosus the furrows are only vestigial, very fine and sometimes they do not oppose each other (due to preservation ?). However, upon closer inspection, especially of well focused photographs on high-contrast paper and darkly printed pictures, these furrows can sometimes

be discerned. Hence, Størmer's interpretation seems valid, on the basis of indepdent demonstration. Whittington is probably correct in concluding that Størmer's material does not reveal the furrow. Hence Størmer's conclusions as to its presence were largely intuitive, albeit vindicated by further study.

The formation of the cephalic segmental furrows is here divided into three steps. In the first of which the furrows are simply parallel on the pleural lobes (pl. 2, fig. 1-5); in the second the furrows fuse to form introfurrow ridges (pl. 2, fig. 6-10); in the third the furrow and ridges have all disappeared, and the surface is smooth (pl. 2, fig. 13-18). Similar morphologic changes are demonstrated by the formation of the pygidial furrows. These steps are illustrated by Cryptolithus bellulus (pl. 20, fig. 10-13) where the first two steps are well demonstrated; figs. 10 and 11 correlate with the first step, and figs. 14 and 15 represent the first step, and figure 16 is the second step. The development of the pleural or fixigenal furrows and the pleural furrows of the pygidium follow an analogous course.

The same steps in the formation of the cephalic furrows are also seen in Crepicephalus deadwoodiensis (pl. 8, fig. 28,29). Something comparable is also seen in the formation of the axial lobe of the glabella: in most of the earliest trilobite instars the glabellar rings are impressed by a longitudinal fissure separating the glabellar rings into two or three pairs of nodes. The longitudinal fissure at certain growth stages becomes a fine ridge, which subsequently disappears as the glabellar rings are completed (pl. 2, fig. 7; pl. 10, fig. 7,8; pl. 13, fig. 2,3). The process of obsolescence of the longitudinal fissure is

exactly similar to the obsolescence of the fixifenal and pleural furrows of the pygidium, which pass through a ridge stage followed by disappearance and a smooth surface in maturity.

The longitudinal fissure of the axial glabellar lobe possibly represents a depression along the course of the alimentary canal, and the glabellar nodes the mesodermal compartments or mesoblasts such as are commonly seen in the early embryos of polychaetes (p. 25) and crustaceans (p.51,text-fig. 18).

Some meraspides are distinctly marked with 3 or 4 pairs of nodes on the fixigenal regions; these nodes supposedly correlate with the four post-oral segments (pl. 8, fig. 10-13, and pl. 4, fig. 14). These nodes disappear in the later ontogenetic stages. They may be representative segmental sense organs, similarly disposed organs occur in the early immatures of Xiphosura (p. 63, text-fig. 22A,B,C, So4).

Posterior fixigenal ridges. Moberg (1899) pointed out the presence in Kjerulfia of a faintly raised line, which shows its position corresponds to the course of the posterior branch of the facial suture. Kisaer (1916, p. 81) found "a fine raised line, that runs in an arc from the posterior edge of the eye to the posterior margin of the intergenal rim". In both instances the lines were interpreted as vestiges of fused facial sutures. The same structures are also seen in Elliptocephala, Olenellus, Holmia, and related genera. The vestigial suture theory was supported by Warburg (1925, p. 37), Raw (1936), and Hupe (1952). Most specialists, however, have either rejected or only conditionally supported this interpretation. Beecher (1897, p. 191), Walcott (1916, p. 8), and Raymond (1917, p. 206) thought the suture was in a condition of symphysis,

the real sutures in a condition of fusion. Størmer (1942, p. 137), and Palmer (1957, p. 126) both out rightly reject the interpretation.

Størmer (1942, p. 138) believes that the so-called posterior facial suture is due to the procephalic (ocular) segment bending posteriorly to the distal end of the post-oral segmented pleurae (1st and 2nd) and ending in front of the pre-occipital segment (3rd post-oral segment). Lindström (1901, p. 16) suggested that the ridges or line represent a pre-existing feature prenuncial of the next step in the development of the true facial sutures. Beecher (1897), noting the same phenomenon, thought the ridges represent lines of symphysis - a fused suture. Raw (1936, p. 586) supports Beecher, believing that the posterior fixigenal ridges are the ankylosis of the posterior branch of the facial suture. Whittington (1957, p. 451) argued that the "fixigenal furrows" are really the intrapleural furrows. The formation of the furrows of both the pygidium and fixigena seems (p. 113) to support Whittington's interpretation.

The ontogenetic development of the posterior fixigenal ridge is clearly indicated by the different growth stages. From the para-protaspid to the early meraspid stages (pl. 2, fig. 1-10) the fixigenal furrows are all parallel and curve slightly anterior-laterally from the dorsal furrow to the palpebral lobes, and the 3rd post-oral (pre-occipital) segment bears a pair of broad-based spines pointed posteriorly. In the late meraspid stage the fixigenal furrows are all strongly bent posteriorly, and the pre-occipital segment gradually decreases in width and becomes elevated into a pair of ridges; these ridges extend continuously posterior-laterally through the hind border

to form a pair of intergenal (or metagenal) spines. This morpholic change is possibly due to posterior bending of the procephalic segment. This seems to support Størmer's interpretation.

Some of the instars often bear a pair of ridges or furrows at the sides of the median tubercle of the occipital segment. This feature is especially clearly indicated by olenullids and related forms, and also in Acerocare ecorne (pl. 2, fig. 16; pl. 13. fig. 17-19) as presented by Størmer (1942, pl. 2, fig. 4). This is a possible result of the segment-generating disc or caudal papilla warping forward underneath the posterior marginal border as we have seen in crustaceans (p. 51, text-fig. 18). Hence, this furrow could be homologous with the cervical groove of Crustacea. If this interpretation is acceptable, then the posterior fixigenal ridges are homologous with the mandiblar groove. This explanation would make the "posterior fixigenal ridge" a combination feature of the fused union of bent cephalic segments and a trace of the madiblar and maxillae I segments. The same groove (cervical groove) is possibly indicated by a juncture which lies between the 7th and 8th segments of Xiphosura, and which is the result of the warping of the generative disc (p. 60). Obviously much more detailed study is necessary before this suggestion has substance.

Cephalic spine. Most silicified trilobite larvae have three pairs of marginal spines along the cephalic shield (pl. 2, fig. 20-22, 28; pl. 10, fig. 6; pl. 9, fig. 3-6); these spines may be preserved, one or two pairs lost during ontogeny. Acanthoparipha and Olenelloides have three adult pairs; Holanshina and Diceratocephalus have two pairs, and most ptychopariids lack spines, other than librigenal, in adulthood. The

olenellid cephalic spines were termed procranid, genal, and metagenal by Raw (1927, p. 11). Palmer (1962) proposed anterior, mid-, and posterior fixigenal spines for the ptychopariid forms. Hupe (1960) designates them as fixigenal 1,2,3 from front to rear. These spines are supposedly homologous in olenellid and ptychopariid forms. However, these designations may not apply (or may be only very questionably applied) to all forms, since some shields have only two pairs of apines (Evitt, 1961, pl. 117; Ross, 1951, pl. 81; Whittington, 1959, pl. 11,16,23,26, etc.) or only one pair [pl. 17, fig. 1-3]. It is difficult, if not impossible, to know whether the spines are fixigenal or pygidial, or if fixigenal, which. Therefore the general terms anterior, lateral, and posterior marginal spines are recommended without any implied homologies. Størmer (1942, p. 12) and Palmer (1957, p. 106) both adopt the term "intergenal spine" instead of "metagenal spine" for adult olenellid specimens.

Palmer (1962, p. 88) believes that "the librigenal spine is not acquired by transfer of any one of the fixigenal spines...". As was brought out previously in the present study, the librigeno-rostrum is clearly associated with the procephalon, when it migrates onto the dorsal surface to become the librigenae. The genal spines are essentially to posterior tips of the librigeno-rostrum; hence librigenal spines are derived from the procephalon, and the fixigenal ones are thus necessarily derived from the post-oral segments. The two kinds of spines are of quite different origins and cannot be derived one form the other. Palmer's interpretation of the origin of the genal spine is well supported.

Raw (1937, p. 585) found that the procranidal spines are absent in Holmia Elliptocephala, and Paedeumias, but present in the Olenelloides

cephalon. Therefore, his view was that "the procranidal spines must have reached the genal angle position by evolution and this would necessarily involve also revolution of the anterior branch of the suture in advance of it". He thought the procranidial spines moved to the genal position during evolution. This explanation has no developmental evidence, for all spines remain in constant position throughout ontogeny (pl. 3, fig. 20-31), except that the anterior pair gradually disappears, whereas the lateral or posterior pairs gradually increase in length. The larval spines may be an ecological adaptation, comparable with those of planktonic larvae of polychaetes, crustaceans, mollusks, etc. Contrary to the opinion of most students, they seem to be of little or no phylogenetic significance.

It should be pointed out that "genal spine" is a common term for the spines located at the posterior lateral angle of the cephalon. But the genal spines are of two derivations: one is librigenal, and the other fixigenal. The spines originating from the librigenae should be donmoniated "librigenal spine:, and those from the fixigenae "fixigenal spine". If there is more than one pair of either type of genal spine, they become, from rear to front, 1st, 2nd, 3rd fixigenal or librigenal spines. See, for example, such forms as Sphaerocoryphe cf. granulatus (Angelin) (Harrington, 1959, p. 52, fig.37E), Acanthoparypha perforata Whittington and Evitt (Whittington and Evitt, 1953, p. 74, pl. 13, and text-fig. 18), and the odontopleurids, etc.

6. Formation of the Post-cephalic Segments

The trilobite body segments, located posterior to the cephalon and constituting the thorax and pygidium, are tertiary in origin. These segments have a slightly different origin from those of polychaetes (see below), but are exactly similar to crustaceans; however, in the Crustacea there is no special term for these segments, all are named secondary somites or segments as they are in the polychaetes.

A. Thoracic segmentation

In the crustaceans after the maxillar somites are developed, the segmental generative disc or caudal papilla is reflected underneath the posterior margin of the shield and proceeds to form the post-cephalic segment (text-fig. 18). The more anterior somites, or proximal side of the segmental series, are the earliest formed and early acquire the mature structure. The same phenomenon may occur among the Trilobita, where the generative disc may have undergone the same reflection. In the annelids, on the other hand, the segmental generative disc, or pygidium, does not undergo this deflection process and extends to the extreme posterior end of the body (text-fig. 10).

Although the segmental generative disc of trilobites has never been observed, it may well be present, but since it would lie underneath the shield, it will never be dorsally observable. In adult specimens of Paedeumias yorkense Resser and Howell the skeleton has 14 thoracic segments, a telson, 3 or 4 rudimentary segments, and a small pygidium. Within the 14 thoracic segments the 3rd one is a macrosomite, and the 15th is the telson. These somites remain in constant position during

growth, i.e., the macrosomite is always in the 3rd position and the telson formed during the transition to the holaspis. This organization could be well explained by the hypothesis of a reflected generative disc. In Stubblefield's (Whittington, 1957, p. 44, fig. 11) study of the ontogeneric development of Shumardia pusilla (Sars) a fifth segment was shown to be added to the pygidium after the complete number of thoracic segments had been developed. This would mean that after the proximal side of the pygidial segment is added to the thorax, the distal side gained a segment which would be necessary in order to maintain a constant segmental number in the pygidium. It therefore appears that thoracic segments are developed by transfer from the pygidium during the growth stages; the proximal side of the pygidium gives up segments to the thorax while concomitantly there is distal replacement of pygidial segments from the generative disc. This is known to be the process operative in the ontogeny of the cephalocarid crustacean, Lightiella incisa (Sander and Hessler, 1963, p. 93, fig. 1,2).

Størmer's (1942, p. 130) views on this matter are that "...it is probable that in trilobites the transverse joints between the pleurae of the thoracic segments, or between these and the cephalon or pygidium, are secondary formations crossing the primary segments. Each thoracic pleura probably contains portions of two succeding segments coalesced along the pleural furrows". Raw (1937, p. 580), and Whittington (1957, p. 451) both interpret the fixigenal furrows of the early instars of olenellids and the pleural furrows on the thoracic and pygidial segments as being serially homologous; all are intrapleural furrows, and the intersegmental grooves run along the convex line. As was previously

pointed out herein (p. 116) Whittington's and Raw's view seems valid. Størmer's observation was strongly influenced by the body structures of Xiphosura, and his conviction that trilobites are merostomatous. It is possibly true that the joint of the prosoma and opisthosoma is due to secondary segmentation of a primary segment, but this is not a fundamental pattern. The fundamental process of segmentation has to be primary, the new segments being added to the previous ones along the primary intersegmental boundaries. An alternative interpretation of the secondary segmentation lying between the 7th and 8th segments is that it is a result of under-warping of the segmental disc after the 6th segment was formed in the manner seen in the ontogenetic development of crustaceans (p. 52 , p. 60). According to this view, the 7th and 8th segment of Xiphosura are essentially one segment divided into two halves by the activity of the generative disc (p. 61, text-fig. 21).

B. Pygidial Segmentation

In trilobite systematics the relative size of the pygidium compared with the cephalon has been used as taxonomic criterion. A trilobite is said to be "micropygous", "macropygous" or "isopygous" according to whether the pygidium is smaller, larger, or subequal in size to the cephalon. The pygidium is essentially a fusion of a certain number of post-cephalic segments. A large number of pygidial segments generally correlates with a pygidium of large size; a small number with one of smaller size. Scutellum and Dicranopeltis, etc. are exceptions to this rule. In these genera of few pygidial segments and a very broad marginal fringe create a large pygidium. The smallest pygidium may consist of one

or two segements and a terminal portion, such as in olenellids, redlichiids, Remopleurides, etc.. The largest pygidia contain more than twenty segments, as in phillipsiids, asaphids, and dalmanitids, etc..

The pygidial segmental generative disc would seem to have been located behind the extreme end of the pygidium, or within the terminal zone, since the segments are always concentrically arranged around this portion (pl. 20, fig. 14; pl. 19, fig. 23,24; pl. 9, fig. 32-37). Hence, the segments which lie near the terminal position or distal region are younger than those more proximal. The generative disc supposedly lost its generative power during the end of late meraspid or early holaspid stage after the animal gained the specific condition, just as in the archaic crestaceans Hemimysis and Nebalia (p. 54). The generative disc is apparently homologous with the pygidium of polychaetes and the caudal papilla of crustaceans. The growth zone of the trilobita, or in Crustacea, presumably remained proximal to the caudal furcae which presumably characterized most if not all trilobites despite their rarity in the record. The best record of these caudal appendages is in Olenoides serratus (Röminger) found by Walcott (1912, 1918) from the Middle Cambrian of British Columbia.

IV. PHYLOGENY OF TRILOBITA

Current thought favors a xiphosuran, arachnid affinity for the Trilobita, but the matter is by no means firmly resolved. Trilobites were long considered to be related to the crustaceans, e.g., works of Walcott (1881, 1894), Bernard (1894), Beecher (1895, 1897), Carpenter (1903), Raymond (1920), and others. They considered that the trilobites were true crustaceans of a primitive type, i.e., an early off-shoot from the line leading from the annellids to the crustaceans. This hypothesis was generally supported by paleontologists and zoologists for a long period, and recently Sanders (1957), from his studies of the Cephalocardia, reasserts their crustacean affinity. Butt (1960), from his comprehensive study of the arthropod head structures, is of the same view and proposes a Trilobita-Crustacea major group of Arthropoda (p.131).

The xiphosuran hypothesis was also established early by Dohn (1871), Packard (1880), and many other students who pointed out the general resemblance between the Trilobita and Merostomata, especially between the larval development of Xiphosura ("Limulus") and the larval stages of trilobites. They suggested a genetic relationship between the two groups. Fedotow (1924), Iwanoff (1933), Snodgrass (1938), and Størmer (1942, 1944, 1950) forcefully demonstrated important and challenging similarities between the merostomes and trilobites. The subject was especially studied by Størmer (1942, 1944) working mainly with trilobite morphology. He took sharp issue with the crustacean concept. He felt that the trilobite features which decisively separated them from

crustaceans are:

a. The tri-lobatation of the dorsal shield and tendency to form a styliform telson.

b. The presence of 4 posterior larval or primary somites.

c. Highly ramified intestinal diverticulae.

d. Homologous appendages in the Trilobita and Chelicerata and the absence of trilobitan appendages from the Crustacea.

Among these four criteria he strongly emphasized the contrasting ontogenetic development and appendage morphology between xiphosurans-trilobites and crustaceans. He viewed the supposedly different number of primary somites and allegedly different appendage organization of crustaceans and trilobites as fundamental differentia. Manton and Tiegs (1957) and Manton (1960) strongly supported the Chelicerata affinity of Trilobita.

The present study of the ontogenetic development of trilobites does not seem to support the Xiphosuran hypothesis. The development of trilobites does not appear to be similar to that of xiphosurans, but very closely resembles that of crustaceans. The early crustacean nauplius and trilobite anaprotaspis both possess two primary somites, whereas chelicerats (Xiphosura) larvae have four (Iwanoff, 1933). The result independently supports Butt's (1960) conclusion as to the common Trilobita-Crustacea taxonomic line. The following discussion is mainly a summary of the previously presented data resulting from studies of the ontogenetic development of a variety of invertebrates of possible relevance to the problem of trilobite phylogeny.

1. The Problem of Primary Somites

It is unfortunate that Iwanoff's (1928, 1933, 1944) hypothesis of primary and secondary segmentation of the articulates has been rejected by several authors (see p.45), since ectodermal segmentation exists in both the heteronomic and nonheteronomic polychaetes (p.46), and since both are represented by forms with pelagic and non-pelagic modes of life. Assuredly in the search for reliabel indicators of polychaete primitiveness a morphologic-ontogenetic trait such as segmentation is of greater reliability than mode of life. Whatever the primordial ecology of segmented marine worms, they have undergone many environmental adjustments, while they all show initial ectoderm segmentation followed by mesodermal. To abandon the morphologic-ontogenetic approach to systematics and phylogeny is serious retrogression.

In evaluating Iwanoff's hypothesis that the larval ectodermal segmentation in polychaetes is archaic, the ontogenetic history of certain lower, and possibly, antecedent, groups is pertinent. In the kinorhynchs and priapulids the first segment is the head; the second segment, the neck; the trunk in most species contains eleven segments. The cuticle of each segment is subdivided into one dorsal and two ventral plates, and the cuticle between the plates is very thin and flexible, permitting articulation. The body wall of the kinorhynchs is the epidermis thickened to form longitudinal epidermal cords which bulge slightly into the pseudocoel. It is to be noted that these animals develop without coelom or mesoderm. They are a grade below the coelomates, but superficially they are segments, and are very similar in appearance to the annelid body structure. This "segmentation" is initiated from

the epiderm, and is remarkably like the initial phase of ectodermal segmentation in annelids. It may have genetic-phylogenetic bearing, and, if so, lends support to Iwanoff's idea that this is the primordial annelidan trait.

It is now know that the anaprotaspis of trilobites and the nauplius of crustaceans both consist of two primary segments; a preoral segment and a generative disc or caudal papilla. Contrarily, the early larva or "trilobite" stage (Størmer, 1944) of Xiphosura ("Limulus") has more than two primary somites lying between the preoral segment and the generative pygidium.

2. The Problem of Secondary Segments

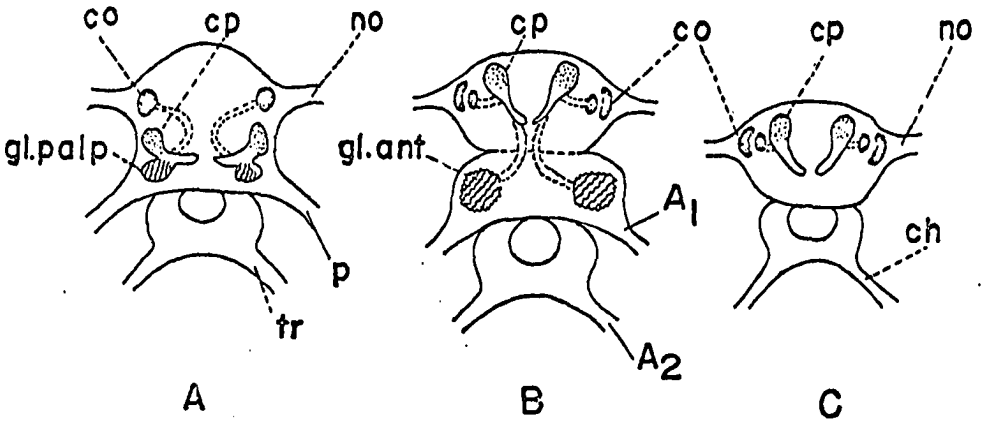
The secondary or body segments in polychaetes are developed from a prepygidial growth zone. Similar development is observed in trilobites and crustaceans. The anterior margin of the generative disc or caudal papilla generates the secondary segments from the teloblasts. In crustaceans, after two secondary segments develop the caudal papilla bends forward beneath the posterior portion of the shield; hence, thereafter the teloblasts of the caudal papilla are essentially located along the posterior margin of the second body segment, and from this new location they continue to generate additional body segments. The same action (generative disc warping) possibly also occurred in trilobites and Xiphosura ("Limulus") although it has not been suggested before. The structure and origin of the occipital segment of trilobites and the post-6th (7th-8th) segment of "Limulus" makes a plausible comparison. Primary and early secondary segments fuse together to form a cephalon.

The additional thoracic and pygidial segments lying between the cephalon, are the true body segments. They are added serially from the teloblasts while the caudal papilla or generative disc moves backward step by step until the animal reaches the adult stage when it is endward with the specific characters. The composite cephalon of trilobites and crustacea comprises five segments whereas the merostome (Chelicerata) cephalon has six or six and a half.

3. The Problem of Cephalic Segments

Ideally, the segmentation of annelids and arthropods is externally delineated by grooves, and each segment has a pair of appendages externally and a pair of coilomic sacs and ganglia internally. The nature of the segments can sometimes be seen from the early stages of embryonic development and may persist during the later growth stages. The internal criteria for the recognition of segmentation is lacking in fossil arthropods where one must rely on groove evidence preserved in the carapace of early instars. The point is made by Butt (1960) that "it is apparent, therefore, that the ideal type of segment marked off by ring-like grooves, with paired appendages, coelomic sacs, and a ganglion just does not exist". This is part of the perennial problem of reconciliation of neontology with paleontology, and while direct comparisons are commonly impossible when criteria pertain to soft parts, an oblique approach may be rewarding.

In the development of many segmented animals, annelids, arthropods, and vertebrates, the young forms often acquire an active existence during the stage of growth when they possess very few segments; these few early



Text-fig. 27: Annellid and arthropod brains: A, a polychaete annelid; B, mandiblate arthropod; C, a chelicerate arthropod. A1, nerve of antennules; A2, nerve of antennae; ch, nerve of chelicerae; co, optic ganglion; cp, peduncular body; gl-ant, antennal ganglion; gl.palp, palpal ganglion; no, optic nerve; p, nerve to first trunk segment. (From Hanström, 1928 after Vendel, 1949.)

segments are often added to the acron in forming an adult cephalon during cephalization. A rather simplified concept of head segmentation has been presented by Hölmgren (1916) and Hanström (1928) and has been elaborated upon by Snodgrass (1938). According to this thinking, the hypothetical head (text-fig. 27) consists of an acron which contains a protocerebrum and a deuterocerabrum (together, the archicerebrum) internally. The mouth is located between the acron and the following segment, the second antennal which contains the tritocerebrum. The tritocerebrum sometimes migrates forward to join with the archicerebrum to form the composite brain, but such forms always retain a commissure passing beneath the stomodaeum. The tritocerebrum represents the first port-oral segment, and the protocerebrum and deutocerebrum represent the eye and antennule respectively. Chaudonneret (1950), on the basis of studies of thysanuaran Thermabia demestica (Packard), concludes that the head comprises 7 segments behind the acron; Weber (1952) was of the opinion, that the archetypical head had 6 head segments behind the acron, and Butt's (1960) modified theory calls for 4 segments behind the acron. The present study of the cephalic segmentation of the earliest trilobites, i.e., anaprotaspis, and related animals seems to be keeping the Hölmgren and Hanström theory.

Text-fig. 27: Annellid and arthropod brains: A, a polychate annelid; B, mandiblate arthropod; C, a chelicerate arthropod, Al, nerve of antennules; A2, nerve of antennae; ch, nerve of chelicerae; co, optic ganglion; cp, peduncular body; gl-ant, antennal ganglion; gl. palp, pdpal ganglion; no, optic nerve; p, nerve to first trunk segment. (From Hanström, 1928 after Vendel, 1949.).

Archicephalon. The archicephalon is the embryonic head of the arthropods which according to Crampton (in Snodgrass, 1938), consists of an acron with eyes and the labral, antennular antenna and mandiblular segments. This structure would correlate with the "ideal head" of Hölmgren and Hanström. In the annelids this would correspond to the prostomium plus two post-oral segments; to the procephalic region (ocular and antennule) and two post-oral segments (2nd and 3rd glabellar segments) of trilobites; to the procephalic region, antennal, and mandibular segments of crustaceans; and to the procephalic region (ocular only, without antennular), cheliceral, and first leg-bearing segment of xiphosurans, not withstanding the arguments of Butt (1960), Manton (1960), and Tiegs and Manton (1958) as to the cephalic segmentation of arthropods.

According to Hölmgren and Hanström's theory, the archicephalon would be composed of the archicerebrum and tritocerebrum (text-fig. 27); however both the anaprotaspis and nauplius larvae have an acron plus primary segments, whereas the "trilobite" stage of "Limulus" has an acron plus three primary segments. If the "trilobite" stage represents an archicephalon, then obviously the archicephalic structure of "Limulus" is not homologous to that of Trilobita and Crustacea. If it is assumed that the chelicerae are homologous with the antennules of crustaceans and trilobites, then the archicephalic structure of the two groups would be similar, for the second and third paired appendages of "Limulus" would then correlate with the antennae and mandibles of crustacea, and the chelicerae with the antennules. This facile explanation is not tenable, however, since embryonic studies by Milne-Edwards (1883), Hanström (1928)

and Johansson (1938) show that the nerves of the chelicerae belong to the ventral nerve cord which is innervated by the secondary brain. They expressed the opinion that the preoral appendages, i.e., antennules, are absent or reduced in "Limulus", whose ontogeny demonstrates forward migration of the primarily post-oral, or cheliceral segments. In the adult the chelicerae attain a distincly preoral position, while the ganglia migrate anteriorly and unite with the preoral brain. Therefore, the deuterocerebrum has apparently disappeared during the forward migration of the tritocerebrum, and certainly no antennules are present on the procephalic region of "Limulus".

The true cephalon of trilobites consist of a procephalon or acron and 4 post-oral segments, which correlate with the prostomium and 4 body segments of annelids; with the procephalic region, antenna, mandiblular, and a maxillary segment of crustaceans; and with procephalic region, chelicera, and 1-3 leg segments of xiphosurans. The xiphosuran cephalon consists of 6 complete and one incomplete (chilarial), segments. Therefore, the 4th and 5th leg segments of xiphosurans correlate with the first two post-cephalic segments of trilobites and crustaceans, and with 6th and 7th segments of annelids (text-fig. 28).

Butt (1960) proposes three main groups of arthropods, which he has defined as follows: In "the first group, the first pair of antennae and a well-formed labrum, second antennae, mandibles, first maxillae and second maxillae are present behind the mouth. This is the group thought to be closest to the trilobites, as indicated by Sanders (1957), Dahle (1956) and others, and includes the class Crustacea. The second great group also preserves the first pair antennae, has a well formed

Polychaeta		Trilobita	Crustacea	Xiphosura
prost.	palpus eye mouth	acron: ant. eye hypo. rost. librlg. lrst glabel - sg. mouth	acron: ant. eye labrum epistome mouth	acron: ant-reduced eye labrum ocellus out- opth-areo mouth
peristomium	seg. 1	leg 1	antennae	chelicerae
	seg. 2	leg 2	mandible	leg 1
seg. 3		leg 3	maxillae 1	leg 2
" 4		leg 4	maxillae 2	leg 3
" 5		thorax	thorax	leg 4
" 6		"	"	leg 5
" 7		"	"	chilaria
" 8		"	"	thorax

Text-fig. 28: Correlation chart showing the head components of the Polychaeta and non-Hexapoda groups of Arthropoda.

Text-fig. 28: Correlation chart showing the head components of the Polychaeta and non-Hexapoda groups of Arthropoda.

Labrum, but the second antennae are very rudimentary or wanting entirely. The mandible, the first maxillae and the second maxillae are present behind the mouth. This group includes the Pauropoda, Diplopoda, Chilopoda and Insecta. In the third great group, the Arachnida, there is no separate head, antennae and antennal lobes of the brain are wanting, the labrum is present and cephalization has taken a rather unusual course, since according to the theory presented here the second post-oral pair of appendages have moved forward around the mouth and also have taken a position anterior to the labrum. Thus, the chelicerae would correspond to the mandibles of the insect."

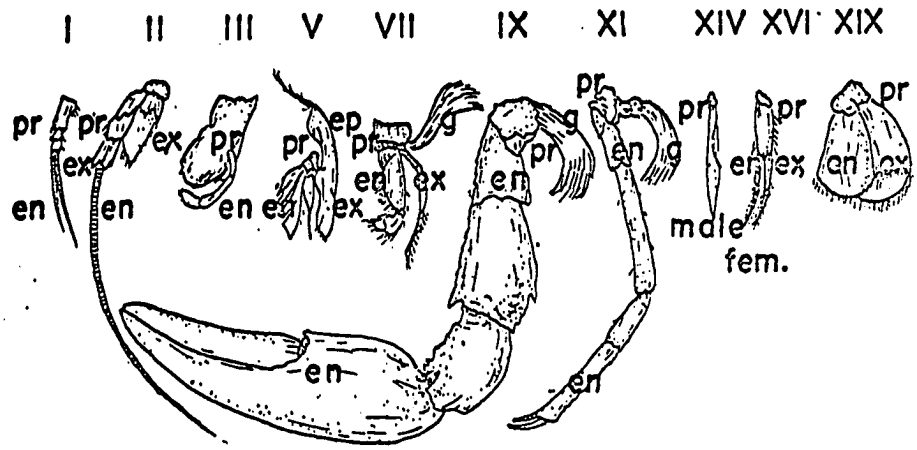
Butt's second group has not come under scrutiny in the present study, but the developmental and anatomical examination of trilobites and limulids supports his views on the major classification of arthropods.

4. The Problem of Appendages

The great studies of trilobite appendages were made by Walcott (1880, 1918), Raymond (1920), and Størmer (1942, 1950). Several genera have revealed well-preserved cephalic and body appendages; among these are: Olenullus, Olenoides, Kootenia, Ptychoparia, Cryptolithus, Triathrus, Phacops, Asteropyge, Ceraurus, Ogygopsis, Flexicalymene, Isotelus, etc. These studies were made by direct examination of natural preservation or by grinding serial sections and reconstruction therefrom.

The appendage structures are especially well shown by Stø rmer (1939, 1942, 1950). All appendages are uniramous; the antennules are simple, whereas the uniramous legs each bear a gill branch (text-fig. 31E). The legs were thought by Beecher (1895), Walcott (1918), Raymond (1920), and Calman (1939) to be biramous structures, corresponding to those of Crustacea. According to this older view, the endopodite and exopodite of crustaceans correspond to the segmented leg and gill branch (epipodite) of trilobites, apparently this is misinterpreted (see p. 141). Garstang (1940) and Heegaard (1945) argued that the differences in structure of the appendages of trilobites and crustaceans are due to an increased development of the protopodite and concomitant reduction of the endopodite segments. Stø rmer in a series papers demonstrates that the trilobite appendage is more closely similar to the appendage structure of xiphosurans ("Lumulus"): both have multiple joints (9 segments, text-fig. 31, A and E) and are uniramous; both possess a gill branch (text-fig. 31, C and E). Stø rmer concludes largely on the evidence that the Trilobita are phylogenetically more closely related to the Xiphosura than to the Crustacea. Sanders (1957, 1959), in connection with his extensive work on the cephalocarid crustaceans, maintains that the triramous (protopodite, endopodite, and exopodite) trunk appendages of cephalocarids are comparable to the trunk appendages of trilobites, and postulates a trilobite origin for crustaceans. Moreover, he believes this triramous structure is the primitive one for all crustacean groups.

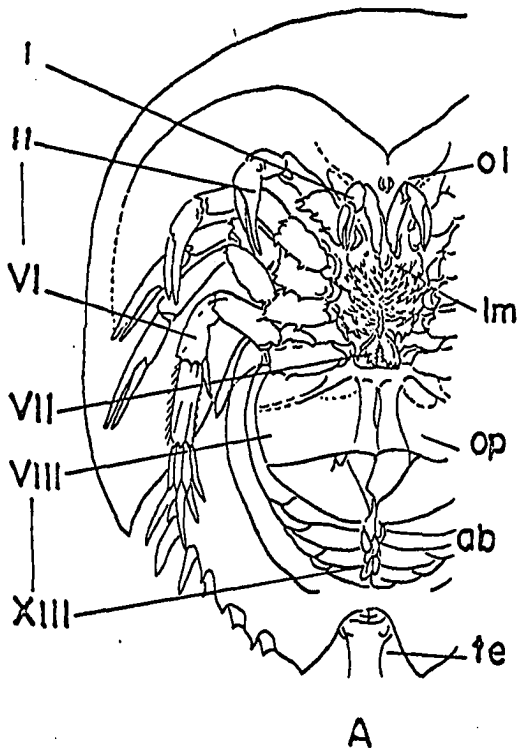
So much of trilobite organization and development now seems to be crustaceous that Sanders' resurrection of the crestacean assignment of trilobites seems highly plausible. There has apparently been far too



Text-fig. 29: Types of appendages of the crayfish (Cambarus). I-II, sensory; III, chewing; V-VII, food-handling; IX, grasping; XI, walking; XIV, male mating; XVI, female egg-carrying; XIX, swimming; pr, protopodite; ex, exopodite; en, endopodite; ep, epipodite; g, gill. (From Storer, 1943.)

Text-fig. 29: Types of appendages of the crayfish (Cambarus). I-II, sensory; III, chewing; V-VII, food-handling; IX, grasping; XI, walking; XIV, male mating; XVI, female egg carrying; XIX, swimming; pr, protopodite; ex, exopodite; en, endopodite; ep, epipodite; g, gill. (From Storer, 1943.)

much reliance of late upon the structure of appendages as fundamental taxobases, especially at a stage when they are still inadequately understood. Moreover, it would be hard to imagine any organs more responsive to ecologic adjustment, more mutable, than aquatic arthropod appendages. Homeomorphy may well be rampant in appendages. Moreover within the appendage series of an individual there is enormous differentiation among the post-trilobites. In higher crustaceans, the same animal body commonly possesses both uniramous and biramous (bifurcate: endopodite and exopodite) appendages, and also both of these appendages may be of quite different shape and structure. The same phenomenon is also found in chelicerates, the prosomal and opisthosomal appendages are not all of the same structure or function. In Cambarus, the crayfish (text-fig. 29, 31), for example, the anterior two pairs of appendages are biramous and have a sensory function; III and IV are uniramous, and serve for chewing and food-handling; V to VIII are biramous and function for touch, taste and food-handling; IX-XIV are uniramous and function for respiration, grasping, walking, and mating; XV to XIX are biramous and function for egg-carrying and swimming. To define the Crustacea as all

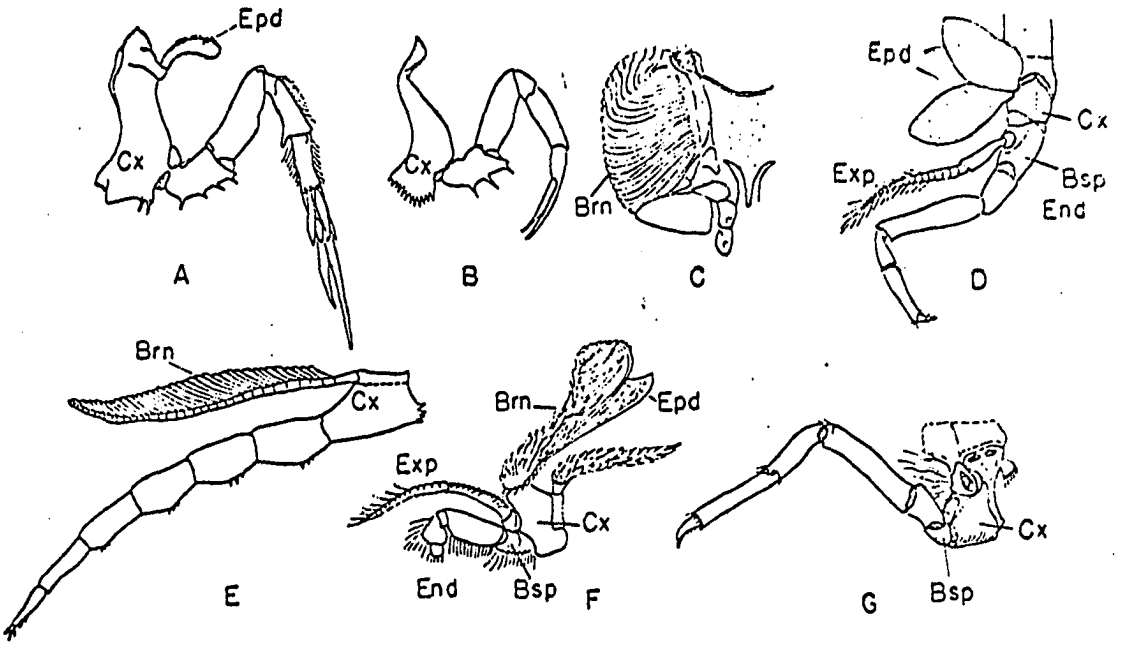


Text-fig. 30: Showing the differentiation of appendages of Xiphosura polyphemus (Linne). I, chelicera; II-VI, chilaria; VIII, opercula; IX-XIII, abdomen; ab, abdominal appendages; lm, labrum; ol, ventral olfactory organ; op, operculaum; te, telson. (After von der Hoeren from L. Fage, 1949.)

possessing biramous appendages is manifestly false. Pelagic and benthonic crustaceans have quite differently constituted appendages. One need only compare isopods, decapods, cirripeds, and phyllopods. The same differentiation occurs in chelicerates. In Xiphosura ("Limulus") (text-fig. 30, 31) the appendages I to V are uniramous, function as grasping, digging, and food-handling, and are quite similar to appendages III and IV of crustaceans. The structure of VIII to XIII of limulids are similar to IX and XII and XV to XIX of crustaceans, because both function for respiration and swimming (text-fig. 29 and 31, C).

Text-fig. 30: Showing the differentiation of appendages of Xiphosura polyphemus (Linne). I, chelicera; II-VI, chilaria; VIII, opercula; IX-XIII, abdomen; ab, abdominal appendages; lm, labrum; ol, ventral olfactory organ; op, operculaum; te, telson. (After von der Hoeren from L. Fage, 1949.)

Returning to the trilobites, the appendages are mostly uniform and uniramous (text-fig. 31, E) except that both anterior and posterior ones are somewhat smaller. Their shapes are similar to thos of walking-legs of crustaceans (text-fig. 29, IX to XI) and xiphosura (text-fig. 31, A, B). This similarity presumably reflects similar function: walking, digging, and food-handling. They also structurally resemble the walking legs of crustacea and the abdominal appendages of Xiphosura (text-fig. 31, A, C) in bearing gill branches, which in all three served for respiration and swimming.



Text-fig. 31: A comparison of the appendages in xiphosurans, trilobites, and crustaceans. A,B,C, Xiphosura appendages of II, VI, and IX; D,F,G, crustacena appendages; D, third left peripod of the crustacean Anaspides; F, left second maxilliped of the crayfish Cambarus; G, third left leg of Cambarus, Brn, branchis; Bsp, basipodite; Cx, coxopodite; End, endopodite; Epd, epipodite; Exp, exopodite. (All redrawn from Snodgrass, 1956.)
E. trilobite appendage.

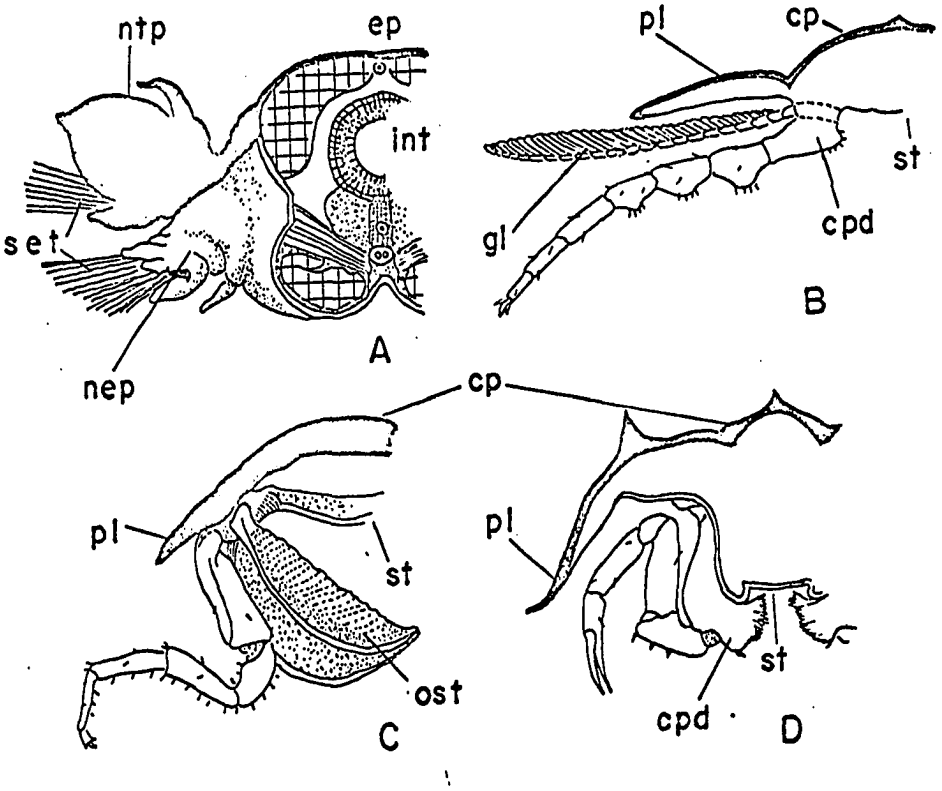
It is assumed that trilobites were non-predaceous and generally walked, dug, and swam along the bottom or burrowed into the substrate; this relatively simple mode of life permitted the retention of the primordial, uniformly simple, appendages. In their serial uniformity and lack of functional differentiation, trilobite appendages are similar to the parapodia of most polychaetes. The trilobite are the most primitive arthropod radical out of which the highly diversified phylum evolved. There took place both serial "differentiation" of appendages, from uniform to polymorphic for different functions, and "simplification" or reduction of the appendage segmental number, required for increased efficiency in the different ecologies which they eventually assumed. "Complication", also occurred, i.e., development of new types of appendage such as the biramous appendage (endopodite and exopodite; text-fig. 31, D, F) of many Crustacea which restrict the gill branches to respiratory function, and consequently a new organ (exopodite) was needed for swimming and cleaning. The exopodite seems to be a subsequent development.

Text-fig. 31: A comparison of the appendages in xiphosurans, trilobites, and crustaceans. A,B,C, Xiphosura appendages of II, VI, and IX; D,F,G, crustacena appendages; D, third left period of the crustacean Anaspides; F, left second maxilliped of the crayfish Cambarus; G, third left leg of Cambarus. Brn, branchis; Bsp, basipodite; Cx, coxopodite; End, endopodite; Epd, epipodite; Exp, exopodite. (All redrawn from Snodgrass, 1956.)

Raw (1953) believed that the pleural spines of trilobites were modified appendages, inherited from the polychaetes, thus once having been part of the worm's complicated parapodia. If his hypothesis that the notopodium is homologous with pleural spine is acceptable, then the neuropodium should be equivalent to the uniramous appendage (endopodite), and the epipodite or gill branch located between might correlate with the setae. This would mean that there is no branch to homologize with the exopodite of crustaceans; thus this bifurcated appendage (exopodite) would seem to have been subsequently derived from the uniramous appendage of the crestacean nauplius, in many ways recalling the parapodium of the polychaetes, are a larval adaptation. Their evolution may correlate with the development of the chitinous exoskeleton in the nauplius, whereas the polychaete metatrochophore was naked. For a chitin-sheathed, and consequently heavy, planktonic larva strong swimming organs would be necessary to keep it afloat, whereas cilia satisfied in the polychaete. The ecologic correlation of naupliar appendages is demonstrated by the fact that when nauplii live in water of higher than normal salinity, the appendages are reduced in length, and if in abnormally low salinity, they increase in length and number of setae required to maintain bouyancy*. This would clearly indicate that the weight of the body influences the structure of appendages in these pelagic organisms. Undoubtedly, Natural Selection operated along these lines in the process of appendage evolution. It is interesting to note that Pisione remota also seemingly possess slender, segmented, and

---

*Personal communication, Dr. William A. Spoor, Professor of Biology, Department of Biology, University of Cincinnati.



Text-fig. 32: Showing the correlation of various arthropod pleurae (indicated by solid black) to the notopodium of polychaete. A, the polychaete, Neries; B, section of thoracic segment of a trilobite; C, section of the second thoracic segment of crustacean, Ligydia; D, section of prosoma behind the third leg of Xiphosura. cp, carapace; cpd, coxapodite; ep, epidermis; gl, gill; int, intestine; ntp, notopodium; nep, neuropodium; ost, ostegite; pl, pleuron; st, sternum. (Modified from Snodgrass, 1938, 1956.)

Text-fig. 32: Showing the correlation of various arthropod pleurae (indicated by solid black) to the notopodium of polychaete. A, the polychaete, Neries; B, section of thoracic segment of a trilobite; C, section of the second thoracic segment of crustacean, Ligydia; D, section of prosoma behind the third leg of Xiphosura. cp, carapace; cpd, coxapodite; ep, epidermis; gl, gill; int, intestine; ntp, notopodium; nep, neuropodium; ost, ostegite; pl, pleuron; st, sternum. (Modified from Snodgrass, 1938, 1956.)

bifurcate appendages (p. 31, 33, text-figs. 11 and 12).

5. Polychaete Origin of the Trilobita

It was the view of Raw (1953) that trilobites are the most primitive arthropods, the true protarthropods, and that they occupied an organizational stage between polychaetes and euarthropods. He said: "Their primitive nature is indicated by: I. the uniformity of the segments and appendages throughout the body; II. the retention of pleura throughout the body unreduced; III. the retention of a large hypostoma and, IV. the retention of soft ventrum". These characters of trilobites and of certain other arthropods indicate a derivation of the class from a polychaete, and quite probably from an archaic polychaete. This theory of trilobite origin is wholly compatible with the observations made in the present investigation. Raw's five hypothetical stages in the transition from annelid to trilobite and arthropod (phyliodocid-life, merocyclism, early protarthropod, late protarthropod, and deutarthropod stages) are, of course, unsubstantiated, but his is an ingenious and stimulating hypothesis.

The study of the ontogenetic development of polychaetes is of great significance in tracing both the ontogeny and phylogeny of trilobites. Åkesson (1961) has found an amazing polychaete in the North Sea, Pisione, which looks quite similar to a Lower Cambrian olenellid trilobite. The mode of ontogenetic development of this animal leads one to speculate that the early larval development of the Lower Cambrian trilobite must be recapitulatory of an adult polychaete of the general Pisione organization (text-fig. 11, 12).

The early pelagic embryos of Pisione have a prostomium in front of a few body segments; as metamorphosis continues, the animal assumes a benthonic mode of life; whereupon the first three body segments gradually migrate forward and fuse with the prostomium to form the head. During this process the prostomium is elongated and the mouth is warped beneath the head, and the eyes are stretched and elongated to form a pair of sickle-shaped eye-rings. This head structure is very similar to the adult form of Olenelloides and to immature stages of olenellids such as Olenellus, Laudonia canadiensis (p. 173, pl. 3, fig. 20-31), Paedeumias, Elleptocephala, etc. If Pisione also secreted a calcium-phosphate tergal carapace it would be virtually indistinguisable from olenellids, especially Olenelloides. This discovery may render Raw's hypothetical transition stages unnecessary. This interpretation of Pisione would seem to be strengthened by the fact that the olenellids and this new annelid seem to share similar modes of life. Both were larvally pelagic and ephebically benthonic. The main difference is that the olenellids developed a thin exoskeleton, whereas Pisione does not. However, this difference is probably not of major importance. Paleontologists have not found any early protaspides of olenellids, in contrast with other trilobites; moreover, adult olenellids have very thin exoskeletons. Apparently the shell secretion of olenellids was both delayed and slow and closely correlated with the ontogenetic change in their mode of life.

6. On the Major Classification of Trilobites

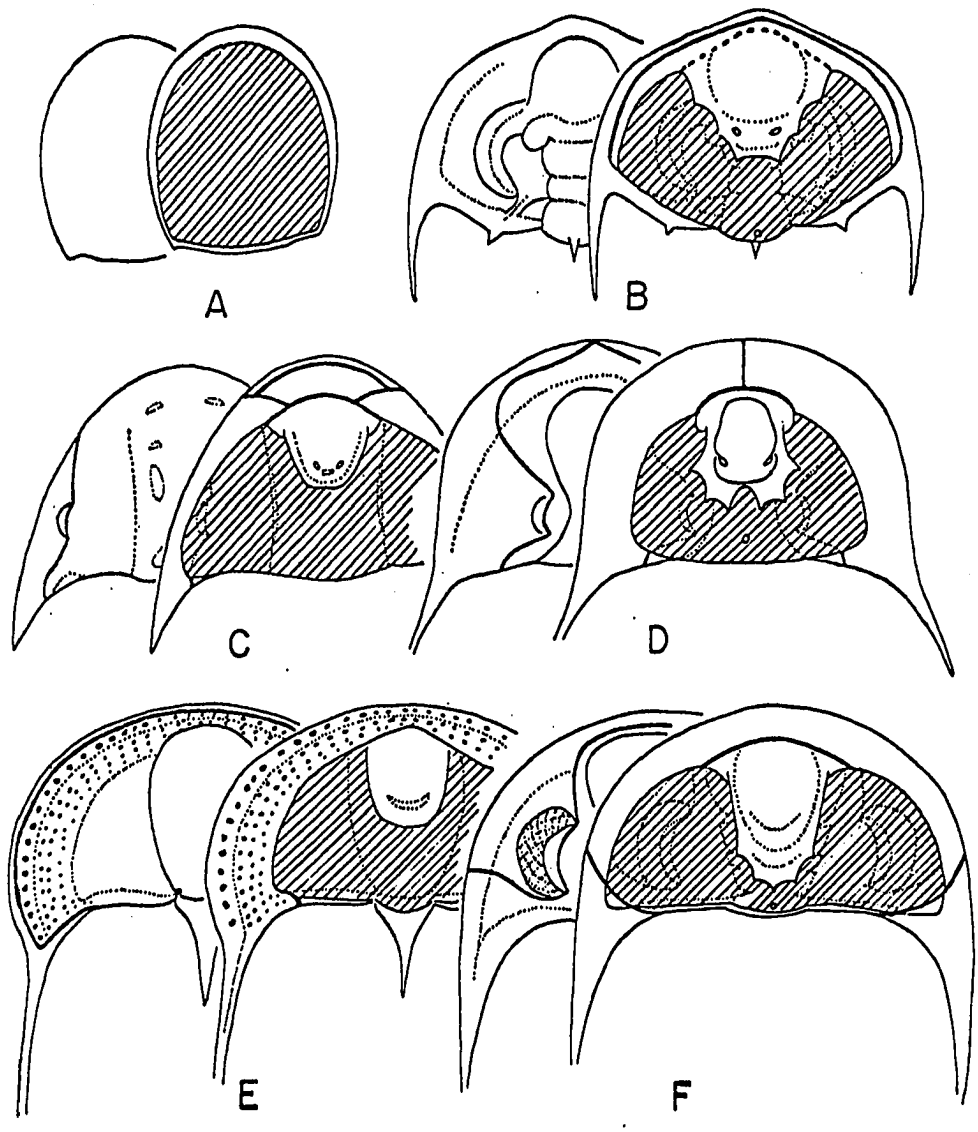
It is the concensus here that a sound taxobasis for major subdivision of the Trilobita has yet to be presented. The discovery of the

interesting ontogenetic relations of the librigeno-rostrum, whether undivided or diversely separated (text-fig. 33), offers the basis for a new, and perhaps fundamental, regrouping. Five categories based on these traits are listed below. Further study may elevate them to taxa.

A. Monorostraloid group. In this group the librigeno-rostrum is a narrowly crescentic perrostrum, which lies underneath the anterior half of the cephalon. It has submarginal and hypostomal sutures. Examples: Olenellus, Elliptocephala, Nevadia, Holmia, Olenelloides, Callavia, Kjerulfia, Wanneria, etc. These are mostly Olenellidae. This group of trilobites is absent (or unknown) from the Oriental region. The geologic distribution is limited to the Lower Cambrian.

B. Trirostraloid group. Here the librigeno-rostrum is divided into three parts: the rostrum and paired librigenae; these parts are separated by the hypostomal, connective, and facial sutures. Examples include Redlichia, Paradoxides, the ptychopariids, Conocoryphe, Aphelaspis, Cedaria, Proetus, Oryctocephalus, Dunderbergia, Flexicalymene, Scutellus, etc.. This is the dominant group among the trilobites, having the greatest geographic and geologic distribution. The librigeno-rostral structures of certain Lower and Middle Cambrian forms (Redlichia, and certain corynexonechids) are well known, but the most of the forms are unknown.

C. Birastraloid group. The librigeno-rostrum is separated into two parts: paired librigenae only; median, hypostomal, and facial sutures are present. No rostrum is present. In this group belong: Bathynotus, Pterocephala, Housia, Norwoodella ?, the asaphids, Xenostegium, Theodenisia, Remopleurides, Menoparia, Homalopyge, etc.. The earliest known birastral trilobite is Bathynotus from the Middle Cambrian of



Text-fig. 33: Showing cephalic structure (solid line) in relation to the librigeno-rostrum. A, Architrilobitoid; B, Monorostraloid; C, Trirostraloid; D, Birostraloid; E, F, Holorostraloid. Rules areas represent the empty cavity of the Cephalon as seen from the center. (Redrawn from Harrington, 1959.)

Text-fig. 33: Showing cephalic structure (solid line) in relation to the librigeno-rostrum. A, Architrilobitoid; B, Monorostraloid; C, Trirostraloid; D, Birostraloid; E, F, Holorostraloid. Ruled areas represent the empty cavity of the cephalon as seen from the center. (Redrawn from Harrington, 1959.)

North America, but the dominant forms are the asaphids which were world-wide in distribution during the Ordovician period.

D. Holorostraloid group. The librigeno-rostrum is here a single plate, without any separation; it is limited by the hypostomal and super-marginal or grande sutures. This group contains the illaenurids, Hungia, Loganopeltis, Lauzenella, Levisella, the nileids, Entomaspis, the trinucleids, phacopids, dalmanitids; and possibly Triarthrus, Peltura, etc.. The earliest known trilobites of this group are Levisella, Hungia, and possibly Peltura from the upper-most Cambrian, but the dominant forms are trinucleids, dalmanitids, and phacopids, of world-wide distribution from the Lower Ordovician through the Devonian.

E. Architrilobitoid group. The rostral plate of certain agnostids is very similar to that of olenellids or certain holorostraloid forms (the rostrum of the eodiscids remains unknown), but the body structure and the ontogenetic development of this group are entirely different from those of typical trilobites (see p.72). Resser (1938) placed all agnostids in a separate subclass, equal in rank to the Trilobita; however, he gave no reason for this move. Comparison of the cephalic structure of this group with that of typical trilobites shows that agnostids have four cephalic segments whereas typical trilobites have five. Hence, the agnostids differ from typical trilobites not only in ephebic morphology but in ontogenetic development. There is a growing tendency to separate them into different classes. The relationship of trilobites to agnostids is much like that of polychaetes to

archiannelids.*

7. Remarks

In many trilobites the librigenal structures remain unknown, especially for the Middle and Upper Cambrian "ptychopaiids". Recently Rasetti (1952) reviewed the literature on this problem and suggested that if the ventral structures were well understood, they might give great insight to both phylogeny and taxonomy of trilobites. Richter (1932) and Stubblefield (1938, p. 411, fig. 2) showed that the rostrum tended to become reduced in size and the librigenae ultimately met so that the connective suture became a median suture. They suggested that this eventually disappeared. There seems to be no ontogenetic evidence to support this hypothesis. Instead, it appears that the tri-, bi-, and holorastraloid types derived from the monorostrum or perrostrum of the olenellid form. Silicified materials of Dunderbergia ? anyta and Dytremacephalus granulosus show protaspides with a single rostrum and a spiny hypostoma. This early condition of the librigeno-rostrum is exactly like that of the perrostrum of olenellids; during the later growth stages the rostrum divided into three parts: the rostrum and paired librigenae. In asaphids, the development of the rostrum is the same as that of D. anyta, and D. granulosus; the early protaspis has a

---

* It should be pointed out that some of the geologically later trilobites: such as trirostraloid and birostriloid forms have their librigenae or librigeno-rostrum so fused together as to create a pseudo-holorostraloid condition in the adult stage. This is seen in Oryctocephalus, the proetids, phillipsiids, and some illaenids. This feature is indicated by the ankylotic ridges along the position of the suture lines. This is the secondary character is not included in the present taxonomic category.

single rostrum which later separated into two parts. In the development of Calliops strasburgensis, the rostrum lacked any separation throughout the trilobite's life. No such recapitulation of the phylogenetic development of the rostrum such as was suggested by Warburg (1925), Richter (1932), and Stubblefield (1938) has been observed.

In any case, the data on the structure of the librigenae are very obscure; more study of this structure is badly needed, both for mature and immature forms. Both silicified preservation and shale specimens can be most revealing.

Much of the adult similiarity between trilobites is apparently convergence or homeomorphy. It may be that librigeno-rostral features will be exceptionally useful in sorting out true from apparent relationships. Note, for example, the similarities, probably bespeaking similar ecologies and convergent morphologies, between olenellid (monorostraloid) and redlichiids and zacanthoidids (trirostralloid) or the similarity to the remopleurids (birastraloid); nileids (holorostraloid) to illaenids (trirostraloid), etc.

V. SYSTEMATIC PALEONTOLOGY

Family Spinagnostidae Howell, 1935

Genus Kormagnostus Resser, 1938

Kormagnostus simplex Resser

Pl. 1, fig. 1-14 and text-fig. 34

Kormagnostus simplex Resser, C.E., 1938, p. 49, pl. 9, figs. 11-13; Rasetti, F., 1945a, p. 444, pl. 69, figs. 32-34; Palmer, A. R., 1954, p. 718, pl. 76, figs. 8-12; Lochman, C. B. and Hu, C. H., 1960, p. 822, pl. 99, figs. 5-31.

K. harlanensis Resser, C. E., 1938, p. 49, pl. 10, figs. 11, 12.

K. esterius Lochman, C. B., 1940, p. 24, pl. 2, figs. 32-35; Lochman, C. B. and Duncan, D., 1944, p. 77, pl. 5, figs. 15, 16, and p. 141, pl. 12, figs. 13-18; Lochman, B. C., 1950, p. 348, pl. 51, figs. 6-9.

K. splendens Lochman, C. B., 1940, p. 25, pl. 2, figs. 23-31.

Diagnosis. Cephalon regularly convex. Glabella conical, convex, with rounded posterior margin and a pair of paraglabellar nodes at the base. Occipital ring narrow, curving backward along the posterior margin of the glabella. Dorsal furrow deeply marked. Pleural lobes strongly convex, with a very broad preglabellar field. Marginal border wide and convex, separated by deep and broad marginal furrow. Two thoracic segments, broad axial lobe and shorter pleural bands, pygidium with strongly convex axial lobe and borad concave marginal furrow. Axis expanded slightly posteriorly. Dorsal furrow well defined. Marginal border wide, moderately convex, with a pair of short blunt spines.

Surface finely granulose.

Description. The cephalon is strongly convex, with a conical glabella and broad preglabellar field and marginal brim. The glabella is delimited by a dorsal furrow, and divided into three axial rings by faint glabellar furrows; the frontal lobe or the first glabellar ring, is transverse, subquadrate, and has a pair of anterior pits at the postero-lateral corners; the second axial ring is narrow and bears a median tubercle; the third axial ring is longer and triangular with a rounded posterior margin. The occipital ring is represented by a pair of triangular base lobes or paraglabellar lobes is situated at the posterior lateral corners of the glabella. The preglabellar field is occupied by a low indistinct median boss immediately anterior to the glabellar margin. The cheeks or pleural lobes are rounded, convex, broad anteriorly and narrowing posteriorly; a pair of faint palpebral ridges extend laterally from the anterior pits; the marginal furrow is concave, broadly arching forward and narrowing postero-laterally; a median notch is directed to the anterior margin of the preglabellar field; the marginal border is medium-narrow, convex, and without a marginal spine.

The thoracic segments are narrow, and convex, with a broad axial lobe and short pleural bands; the axis is moderately convex; the pleural bands are distinctly marked by pleural furrows, and the ends of the tips are directed slightly anteriorly.

The pygidium is quadrate in outline and strongly convex. The axial lobe is divided into three rings by a faint furrow; the first ring is narrow and arches slightly anteriorly; the second is of the same nature as the first one, except that it bears a median tubercle; the last ring

is broad, semicircular and expanded both slightly laterally and posteriorly. The dorsal furrow is distinct. The pleural lobes are narrow, tapering posteriorly and downsloping laterally to the broad, shallow marginal furrow; the marginal border is of medium width, convex, with a pair of short blunt spines directed posteriorly from the posterior lateral corners.

The surface is covered with minute granules.

Remarks. This species is represented by more than 30 immature and mature specimens, all recovered from a few pieces of light-grey, medium-crystalline limestone. The smallest instar is about 0.30 mm. long (sag.) and the adult forms are more than 3.00 mm. The smallest pygidium is 0.40 mm. long, and the larger ones are 2.30 mm. in length (sag.); arranged in order of size, they show a continual growth sequence. In the growth stages, the pygidium shows more morphologic change than the cephalon; the pygidial axis, which in the meraspid stage is conical in form and largely separated from the posterior marginal border by the pleural lobes, develops first into a subquadrate form and then into a posteriorly expanded form, separating the pleural lobes and abutting the posterior marginal border. The glabella develops from a conical to a truncate-conical form; and the median furrow disappears in the larger cephala.

As seen in the synonomy, some of Resser's (1938) and Lochman's (1940) "species" are here interpreted as representatives of different growth stages of K. simplex Resser. K. simplex Resser (U.S.N.M. 94842) and K. esterius Lochman, both with largely expanded pygidial lobes, are the adult forms, and the K. harlanensis Resser (U.S.N.M. 94863) and K.

splendens Lochman (U.S.N.M. 98697), both developed with smaller narrower pygidial axis, are possibly the respectively late and earlier mature forms. Although the conditions of preservation may also have influenced the form in the types of these "species", it seems more likely that they represent different growth stages of a single species.

The agnostid orientation employed here is that urged by Raymond (1917, 1924, 1925) and supported by Kobayashi (1935). Raymond reversed the generally accepted orientation of these trilobites, uring that: 1) pleural extremities should point posteriorly, and 2) the "ventral plate" appears to be separated from the dorsal shield by a suture. Kobayashi (1935, p. 75) showed, 1) that in the Condylopygidiae which are primitive agnostids, the pleural extremities point posteriorly; the forward bending of later forms was apparently an adaptation which aided in enrolement. Moreover 2) a "ventral plate" has been found on both shields in one agnostid species by Westergard and Holm (1930) who, however, regarded their "plates" as doublures.

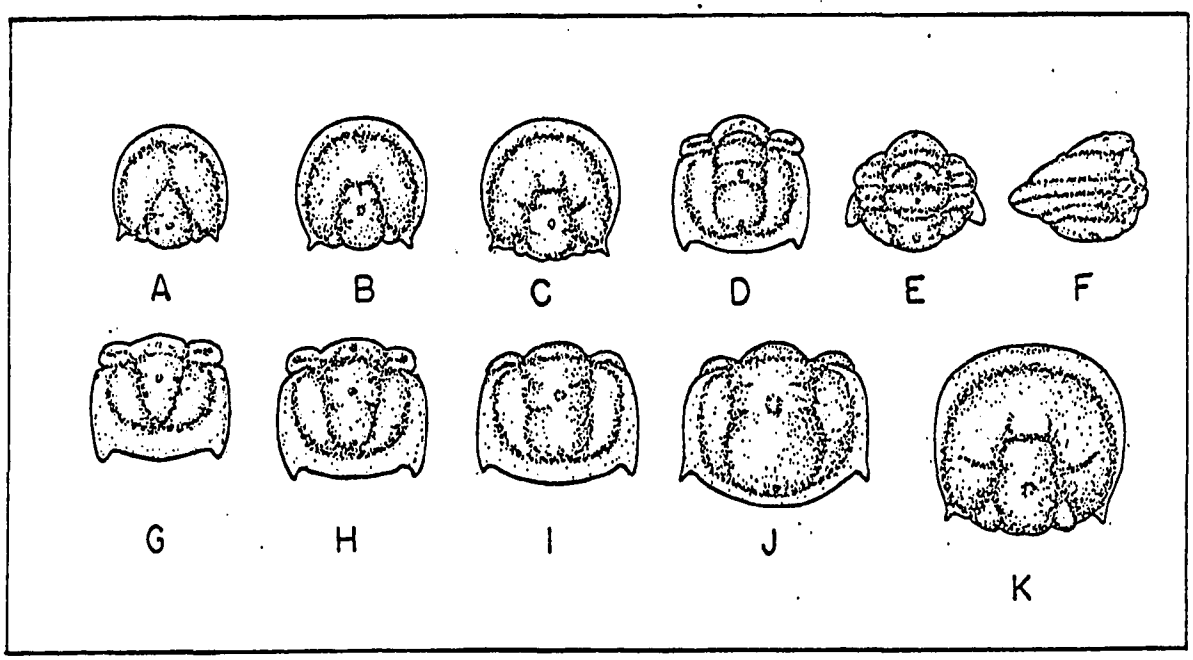
In the course of the present study, it has been observed that the cephalon of K. simplex shows a pair of ridges extending laterally from the anterior pits (pl. 1, fig. 5, and text-fig. 35K). They are presumably palpebral ridges and their presence supports the Kobayashi's interpretation as to agnostid orientation.

Horizon and Locality. Upper Cambrian, Cedaria zone, Bonneterre Dolomite, Southern Bonneterre, St. Francois County, Missouri.

Figured specimens. Complete skeleton, U.C.M. 38722.

Cephala, U.C.M. 38722a-e.

Pygidia, U.C.M. 38722f-k.



Text-fig. 34: A growth sequence of Kormagnostus simplex Resser. A,G,H, early meraspides, A, cephalon, x 53; G,H, two pygidia each associated with one thoracic segment, x 35, x 34; B-F,I, late meraspides, B, cephalon, x 30, C-F, dorsal, posterior, and side views of a complete specimen, x 17; I, pygidium, x 30; J,K, top views of a cephalon and a pygidium, x 13 x 8. (Drawings made from photographs.)

Kormagnostus simplex Resser, ontogeny

Early meraspid stage (pl. 1, fig. 1, 6-8 and text-fig. 34, A,G,H). The cephalon is spherical convex and about 0.30 mm. in length (sag.). The glabella is subtriangular, elongate, conical, and restricted to the posterior half of the shield; glabellar furrows are not distinctly marked; the preglabellar field is marked by a longitudinal furrow. The marginal border is narrow and separated by a marginal furrow.

The pygidium is convex, quadrate-spherical in outline, and about 0.40 mm. in length. The axial lobe is conical, tapering posteriorly; the axial furrows are not distinctly marked; the median tubercle is borne at the mid-length of the axial lobe. The dorsal furrow is distinct. The pleural lobes are about one-half as wide as the axis, convex, tapering slightly posteriorly. The marginal furrow is distinctly impressed and with the dorsal furrows at the posterior margin of the axial lobe; the marginal border is flat, broad, and tapers anteriorly. Figures 6 and 7 show a pygidium associated with one thoracic segment.

The surface of the skeleton is rough, being covered by fine granules.

Later meraspid stage (pl. 1, fig. 2-4, 9,10,12-14 and text-fig. 34 B-F, I). The cephalon is convex and about 0.50-1.20 mm. in length (sag.). The glabella is truncate-conical. The preglabellar field is occupied by a small, slightly convex median boss immediately in front of the glabella. The pygidium is subquadrate, convex, with a broad marginal brim. The axial lobe is cylindrical, with a rounded posterior margin; the first axial ring is narrow and transverse; the second is the same as the first one except that it bears a median tubercle; the third ring is

rounded and extends to the posterior marginal furrow. The pleural lobes are rather narrow, tapering posteriorly, and ending at the sides of the posterior lateral margin of the axial lobe. The marginal furrow is broad and concave; the marginal border is broad, slightly upturned from the marginal furrow and bears a pair of spines at the posterior lateral margin.

The surface is covered by fine granules.

The important features of this stage is the absence in the preglabellar field of a median furrow and the presence of the median boss. The glabellar furrows have first become distinct; the pygidial axis becomes subquadrate to cylindrical and the lateral lobes are narrower than previously.

Figured specimens. Early meraspides. U.C.M. 38722a,f-h.
Late meraspides, U.C.M. 38722.
38722b-d,i,j.

Family Pagetidae Kobayashi, 1935

Genus Pagetia Walcott, 1916

Pagetia clytia Walcott

Pl. 1, figs. 15-32 and text-fig. 35

Pagetia clytia Walcott, C. D., 1916, p. 408, pl. 67, figs. 2, 2a-e.

Pagetia (Mesopagetia) clytia Walcott, Kobayashi, T., 1944, p. 63-66, pl. 1, fig. 14.

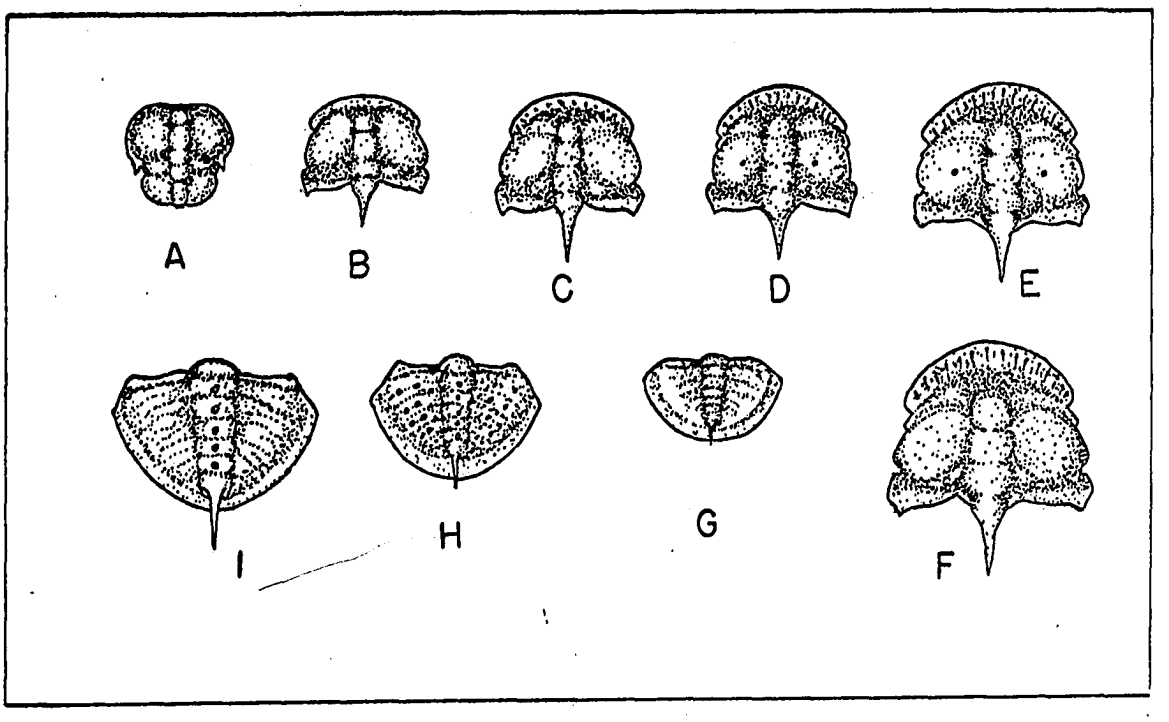
Diagnosis. Skeleton elongate-ovate, convex. Cranidium having broad, flat marginal fringe and stout occipital spine. Glabella slenderly conical, with two pairs of glabellar furrows. Palpebral lobes small. Proparial facial suture. Pygidium slightly convex, 6 or 7 axial rings, each bearing a tiny median tubercle. Pleural lobes divided into pleural bands. Marginal border narrow, flat, and smooth. Surface finely granulose.

Description. The cranidium is rounded in outline and moderately convex. The glabella is slenderly conical and divided into three glabellar rings; the first glabellar ring is convex and triangular; the second is narrowly transverse; and the third large, broad, and slightly convex. The occipital furrow is deep along the sides of the glabella and shallow across the axial line; the occipital ring is posteriorly convex and bears a stout posteriorly directed spine. The dorsal furrow is broad and deeply marked. The anterior brim is broad, concave, without clearly separated preglabellar field and anterior furrow; the anterior border is broad, flat, and fringe-like, with many elongate radial pits. The flat fixigenae are slightly wider than the glabella

and slightly upturned; a pair of tubercles occurs on the posterior-lateral area of the fixigenae near the marginal furrow; the palpebral ridges are faint and curved anteriorly; the palpebral lobe is narrow, medium sized, and located opposite (tr.) the mid-line of the glabella; the posterior fixigena slope steeply downward and have geniculate posterior-lateral borders. The posterior lateral furrows are deeply marked and broad, running anterior-laterally before reaching the side margins. The anterior branches of the facial suture are strongly divergent and the posterior branches normal to the sagittal line.

The pygidium is triangular in outline and highly convex along the axis; the axial lobe is divided into 6 or 7 rings by distinctly marked ring furrows; a median tubercle occurs on each axial ring; the terminal portion is triangular with a long, posteriorly directed spine. The pleural lobes are convex, sloping down to the narrow, flat marginal border; 5 or 6 pleural segments are distinctly separated by fine inter-pleural grooves; the pleural furrows are wide and deeply impressed. The surface is covered by granules.

Remarks. This species is represented by more than 80 immature and mature specimens; all were recovered from a few pieces of dark grey, medium crystalline limestone. The smallest instar is approximately 0.30 mm. in total length (sag. fig. 23), and the mature forms are about 2.0 mm. long (exclusive of the pygidium). This species differs from P. bootes Walcott, P. (Eopagetia) resseri Kobayashi, and P. maladensis Resser in having a narrow, concave preglabellar field without any median furrow; it should be pointed out that the small forms of the present species all show a wide preglabellar field and occupied by a median furrow,



Text-fig. 35: Pagetia clytia Walcott. A, a complete paraprotaspis, x 50; B, an early meraspid cephalon, x 24; C,D,G, late meraspides, C,D, two cranidia, x 26, x 28; G, pygidium, x 25; E,F,I,H, holaspides; E,F, two cranidia, x 14, x 13; I,H, two pygidia, x 13, x 15. (Drawings made from photographs.)

whereas the larger one lack both wide field and furrow. The glabella is made of four rings: a frontal lobe, two axial rings and an occipital ring.

Horizon and Locality. Middle Cambrian, Bathyuriscus-Elrathina zone. Northeast side of road in Santaquin Canyon, Wasatch Mts., Utah.

Figures specimens. Cephala, U.C.M. 38732, 38723i-q.

Pygidia, U.C.M. 38732a-h.

Pagetia clytia Walcott, ontogeny

Paraprotaspid stage (Pl. 1, fig. 23, and text-fig. 35A). The shield is differentiated into cephalon and pygidium and is about 0.30 mm. in total length (sag.). The cephalon is moderately convex, quadrate in outline, with a rounded anterior border. The glabella is slenderly conical with fine but recognizable glabellar furrow. The dorsal furrow is shallow and broad. The anterior brim is deeply concave. The occipital ring is distinctly delimited, possibly bearing a small occipital spine. No thoracic segments are seen. The flat fixigenae are about twice as wide as glabella and are gently upturned from the dorsal furrow, with swollen lateral margins; the palpebral lobes are not known. The posterior lateral border is broad, convex, and separated by shallow, concave marginal furrows. The protopygidium is semi-circular, convex, and steeply downward from the posterior margin of the cephalon; the axial and the pleural lobes are without distinct segmentation.

Early meraspid stage (Pl. 1, figs. 15-17,24,25 and text-fig. 35B). The convex cranidium is quadrate in outline, with palpebral lobes appearing on the dorsal surface. It varies from 0.40-0.50 mm. in length.

The glabella is slenderly conical with well developed frontal lobe, two recognizable glabellar rings, and a posteriorly arched occipital ring. The frontal lobe is triangular, convex, and bearing a pair of well developed anterior pits on the posterior lateral bases. The dorsal furrow is broad, shallow, and deeply impressed. The occipital ring is small and faintly separated by the occipital furrow; the median spine is large, stout, directed posteriorly and has a pair of narrow ridges projecting laterally and anteriorly connected with the fixigenal borders. The preglabellar field is wide and has a longitudinal median furrow. The anterior border is narrow, arching anteriorly and is delimited by the anterior furrow. The convex fixigenae are slightly wider than the glabella, with palpebral lobes located at the mid-line of the glabella (tr.); the posterior fixigenal borders are narrow and geniculate, about the same width as the glabellar base.

The pygidium is rounded, highly convex, with a narrow, flag marginal border; the axial lobe is slightly conical, tapering posteriorly and ending in a terminal spine; the axial rings are not distinctly divided; the convex pleural lobes are twice as wide as the axial lobe and lack distinct pleural furrows. The pygidium is possibly associated with a thoracic segment.

The surface is covered by fine granules.

The specimens of this stage are distinguished from those of previous ones in having a well-developed anterior border, a distinct frontal lobe and anterior pits; the facial sutures are distinct; the pygidium is articulated with one free thoracic segment.

Late meraspid stage (Pl. 1, figs, 18,19,26,27, and text-fig. 35C,B,G).

The cranidium is about 0.50-0.55 mm. in length (sag.) and moderately convex. The glabella is cyclindrical, slightly tapering forward, with a rounded anterior margin, and divided into three glabellar rings by faintly impressed glabellar furrows. The anterior pits and longitudinal median furrow are shallower and have disappeared in the larger specimens. The fixigenae are of the same width as the glabella or slightly wider. The pygidium has faintly marked axial and pleural furrows and does not incorporate any thoracic segments.

Granules cover the cranidal surface and the pygidal pleural bands.

The present stage differs from the earlier one in having a shorter and wide glabella and fixigena of nearly the same width as the glabella.

Figured specimens. Paraprotaspis, U.C.M. 38723i.

Early meraspides, U.C.M. 38723a-c,j,k.

Late meraspides, U.C.M. 38723d,e,m. 38723.

Family Olenellidae Vogdes, 1893

Genus Olenellus Hall, 1860

Olenellus truemani Walcott

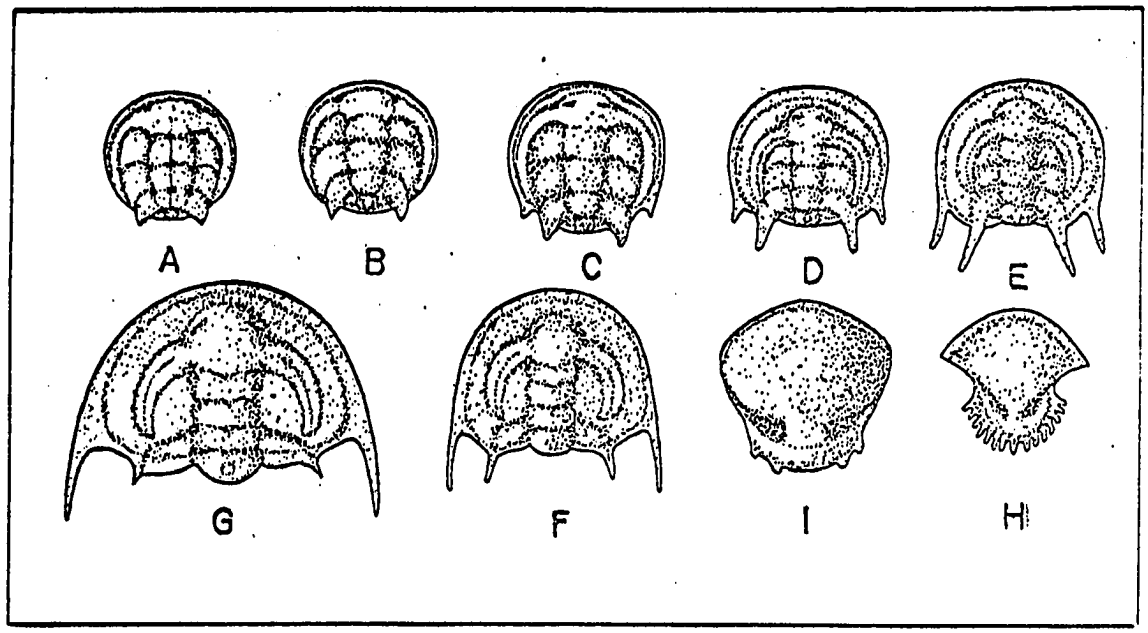
Pl. 2, fig. 1-26, and text-fig. 36

Olenellus truemani Walcott, C. D., 1913, p. 316, pl. 54, figs. 2-10

Olenellus (Olenellus) truemani Walcott, Lochman, C. B., 1952, p. 89, pl. 18, figs. 6-12.

Diagnosis. Cephalon semi-circular in outline, moderately convex; glabella with large, subrounded frontal lobe, and three unequal glabellar segments; dorsal furrow distinctly defined. Palpebral lobe strongly arcuate, running from side of frontal lobe posterior-laterally to occipital furrow. Metagenal spines smaller than genal spines. Preglabellar field narrow, flat, and distinctly delimited by anterior furrow. A faint posterior fixigenal ridge extends posterior-laterally from the pre-occipital segment to the rear margin to become continuous with a short metagenal spine.

Description. The cephalon is semi-circular in outline, moderately convex at the center and uniformly inclined to the ocular platform and preglabellar field. The glabella is cylindrical with a broad and forwardly expanded frontal lobe which is transversely subcircular, convex above the preglabellar field, and bearing a pair of faint lateral furrows; the second glabellar ring is narrower (sag.) and wider than the following; the third ring is medium-sized; the fourth one is larger than the previous ones and broadly chevron-shaped; the occipital ring is the same size as the fourth one and bears a minute median posterior tubercle. The glabellar furrows are all deeply impressed lateral but



Text-fig. 36: Olenellus truemani Walcott. A, paraprotaspis, x 40; B,C, two early meraspides, x 25, x 30; D,E, two late meraspides, x 17, x 15; F,G, two holaspides, x 8, x 6; H, an early meraspid hypostoma, x 10; I, a late meraspid hypostoma, x 3. (Drawings made from photographs.)

shallow across the axis. They are directed posterior-laterally from the dorsal furrow. The occipital furrow curves posteriorly and is deep laterally and shallow axially. The dorsal furrows are distinctly impressed laterally but absent at the lateral marginals of the frontal lobe. The fixigenae are elongate, semi-ovate, gently convex, and delimited by fine and shallow palpebral furrows. The palpebral lobes are parenthesis-shaped and extend posterior-laterally from the lateral bases of the frontal lobe, to the rear fixigenae, but terminate before reaching the posterior borders. The eye rings are vertically disposed and extend the full length of the lobes. The occular platform is slightly broader both anteriorly and posteriorly than medially. A narrow marginal furrow runs continuously around the cephalon. It has a median notch towards the preglabellar field; the marginal border is narrow, convex and continuous with a pair of short, slender genal spines. A faint posterior fixigenal ridge extends from the side of pre-occipital ring posterior-laterally to the hind fixigenal border, then curves backwardly, crossing the posterior border to from the metagenal spine.

The hypostoma is roundly triangular in outline, with a strongly convex median body, which is triangular in plan with the anterior region arching forward. The hypostomal maculae are deep and narrow, extending posterior-laterally from the lateral borders; the rear lobe is crescentic, conves, curving posteriorly, with a rather narrow marginal border.

The surface of the skeleton is covered by a fine irregular reticulum of ridges; a row of distinct pits occurs along the cephalic furrow.

Remarks. This species is represented by more than one hundred immature and mature skeletal fragments; all are prepared from a few

small pieces of dark-grey, finely crystalline limestone. The assignment and relationship of this species were thoroughly discussed by Lochman (1952), where she attributed it to her new subgenus Olenellus. It seems that the Mexico specimens here being presented have a wider preglabellar field and broader fixigenae in comparison to typical (Canadian specimens) representatives of O. truemani. These differences might be due to preservation. The Canadian specimens were deformed, since they are preserved in a shale matrix, whereas the Mexican ones occur in limestone. Discounting discrepancy factors attributable to diagensis and deformation, the Mexican and Canadian material seems to be conspecific. The present form seems to be typically O. truemani Walcott and no useful purpose seems to be served in employing the subgeneric designation of Lochman.

The early instars of this species, which I have judged to represent the paraprotaspid stage, are about 0.45 to 0.60 mm. in length (sag.). They are spherical in outline and strongly convex. The axial lobe is elongate-fusiform and faintly divided into an obscure median fissure along the axial lobe, axial nodes, and cephalic segmental furrows. Due to these unique characteristics of this instar, this seems to be the earliest growth stage yet known among olenellid trilobites.

The early meraspid are possibly correlated with Palmer's (1957) stages I and II, and the late meraspides correlate with his stages III and IV, judged both from their morphology and size.

Horizon and Locality. Buelina Formation, Lower Cambrian, near Caborca, northwestern Sonora, Mexico.

Figured specimens. Cephala, U.C.M. 38724, 38724o-q.

Hypostoma, U.C.M. 38724v

Fragments, U.C.M. 38724x-z.

Olenellus truemani Walcott, ontogeny

Paraprotaspid stage (Pl. 2, figs. 1-5 and text-fig. 36A). The shield is about 0.45-0.60 mm. in length (sag.). It is characterized by a fusiform axial lobe, longitudinal axial fissure, cephalic segmental furrows, and parenthesis-shaped dorsal furrows. There are three pairs of pits distinctly impressed at the intersection of the dorsal and cephalic segmental furrows. The cephalic segmental furrows are shallow but well defined; they arch slightly forward to the axial lobe and curve backward to the palpebral furrows. The cephalic segmental bands are gently convex, of which the second and third end in the inner palpebral lobes, and the fourth bends laterally and posteriorly to the rear cephalic margin, continuous with a pair of long spines. The last or occipital segment is very short and bears a small occipital ring. The first cephalic segment, or the frontal lobe, is gently convex and rounded, with a pair of palpebral lobes extending from the lateral margin, running posterior-laterally and terminating in front of the fourth cephalic segment. The palpebral lobes are elongate and elevated vertically above the marginal border. The palpebral furrows are distinctly marked. The marginal border is very narrow and concave, broad anteriorly and narrow posterior-laterally. Neither anterior cephalic or genal spines have been observed. The stout metagenal spines show possible association with a small protopygidium at the hind of the occipital segmental border.

Early meraspid stage (Pl. 2, figs. 6,10,20,23, and text fig. 36B,C,H). The shield varies from 0.65 to 1.0 mm. in length (sag.). It is spherical in outline, with moderately to strong convexity. The axial

lobe is divided into a large frontal lobe, three axial rings, and a small terminal ring. The longitudinal furrow is absent. The dorsal furrows are distinctly marked. There are three pairs of pits deeply impressed at the intersections of the cephalic segmental and dorsal furrows. The cephalic segmental furrows are incised laterally but become shallow across the axial lobe. The resulting cephalic segments are gently convex and arc posteriorly to the palpebral lobes; they are elevated above the marginal border and extend from the lateral margin of the frontal lobe, whence they curve posterior-laterally, and end in front of the fourth cephalic segment. No preglabellar field has been observed except for a narrow concave area. The small occipital segment occupies a narrow subtirangular area with a small subrounded occipital ring, which bears a minute, posteriorly directed median node or short spine. Anterior cephalic and genal spine have not been observed. The metagenal spines are long and stout (fig. 23), and extend continuously from the pre-occipital segment.

The convex hypostoma is elongate-subtriangular in outline, with a posterior margin showing 15 dentations. The convex median body is triangular and delimited by deep maculae.

The distinctive feature of this stage is the disappearance of the median longitudinal furrow. The axial lobe is narrower and longer; the marginal border is broader; and the frontal lobe is faint with a pair of furrows.

Late meraspid stage (Pl. 2, figs. 11-14 and text-fig. 36D,E,I). The shield ranges from 1.2 to 1.8 mm. in length (sag.), is rounded in outline and moderately convex. The axial lobe is cylindrical and divided into

five axial rings by furrows; the frontal lobe or the first glabellar segment is rounded with a pair of finely marked, elongate pits at the sides; the second glabellar segment is smaller and narrower than the first and thrid ones; the third glabellar segment is broader (sag.) than the second and fourth ones. The fourth glabellar segment is rounded and triangular; the occipital ring is smaller and distinctly separated by an occipital furrow. It becomes a minute median spine. The dorsal furrow is faint. The distinct cephalic segmental furrows arch posterior-laterally to the palpebral furrow; the pre-occipital segment extends laterally and posteriorly to become continuous with a pair of metagenal spines. The palpebral lobes are narrow and crescentic, running from the lateral margin of the frontal lobe to terminate in front of the fourth cephalic segment. The anterior marginal border is narrow and well elevated. The narrow and flat preglabellar field is delimited by a broad, concave anterior furrow. Genal spines are present on the posterior-lateral margin of the shield.

Both the complete hypostoma and the median body are of subtriangular in outline; the median body is more convex than that of the previous stage, but less expanded than that of the holaspis; the posterior marginal dentation has disappeared.

The surface is covered by fine granules.

The important features of this stage are the presence of a pair of genal spines, the cylindrical glabella, and the appearance of the preglabellar field. This stage differs from the holaspid in that the latter has longer genal spines and the cephalic segmental furrows are absent. A pair of strongly elevated ridges extends from the fourth

glabellar segment; they are continuous with a pair of slender metagenal spines. The ocular platforms are of uniform width.

Figured specimens. Paraprotaspides, U.C.M. 38724a-c, e.

Early meraspides, U.C.M. 38724f-j, t, w.

Late meraspides, U.C.M. 38724k-m, u.

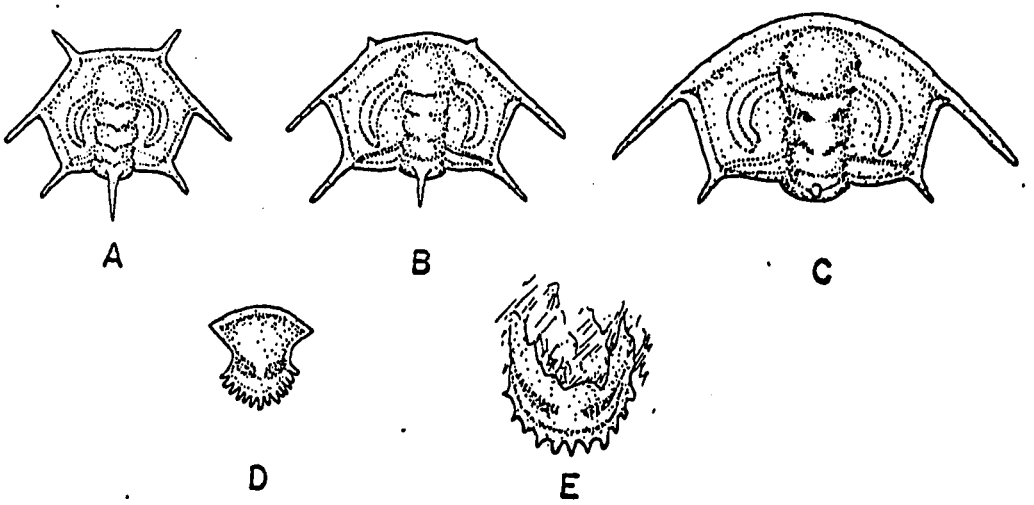
Genus Laudonia Harrington, 1956

Laudonia canadiensis, n. sp.

Pl. 3, figs. 20-31, and text-fig. 37

Diagnosis. Cephalon transversely pentagonal in outline, moderately convex, with roundly arching anterior border, and two pairs of spines which project posterior-laterally from the four corners. Glabella cylindrical with rounded and expanded frontal lobe; three distinctly marked glabellar rings, and a broadly convex occipital ring. Palpebral lobe narrow, elevated above the ocular platform. Marginal border narrow, convex, delimited by marginal furrow. Posterior fixigenae marked with a pair of ridges, which extend laterally from the base of the palpebral lobes and continue into the metagenal spines. Hypostoma prominently convex, with large median body and spinose posterior marginal border. Thoracic segments having long pleural spines and serrate lateral margins. Pygidium unknown.

Description. The cephalon has a transversely pentagonal outline and is moderately convex. The glabella is expanded slightly both anteriorly and posteriorly; the third glabellar segment is triangular and narrower than the fourth one; and the fourth segment is broader (tr.) and larger. The occipital ring is broad and convex, with a median node or short tubercle. The glabellar furrows are separated by the central axis except for the first furrows, which cross the axis behind the frontal lobe. The dorsal furrow is deeply impressed at the sides of the second glabellar ring, but shallower both posteriorly and anteriorly. The narrow palpebral lobes extend in a low arc to the mid-line of the fourth glabellar segment (tr.). The palpebral furrows are deeply impressed.



Text-fig. 37: Laudonia canadiensis, n. sp. A, an early meraspis, x 14; B, a late meraspis, x 10; C, holaspis, x 4.5; D, a late meraspid hypostoma, x 11; E, a broken holaspid hypostoma, x 2.5. (Schematic drawings from photographs.)

The eyes have vertical sides and extend the full length of the palpebral lobes. The inner fixigena is small and half moon-shaped. The outer fixigenae are of medium width, widening slightly anterior-laterally. The posterior fixigenae are narrow, marked with a pair of well elevated ridges, which extend from the fourth glabellar segment laterally and posteriorly to the posterior marginal border, and are continuous with a pair of short metagenal spines. The marginal borders are narrow and convex, distinctly marked off by marginal furrows. The genal spines are strong and porject outwards from the anterior lateral borders opposite the first glabellar furrows (tr.). The metagenal spines are slender and extend posteriorly and laterally.

The hypostoma is subtriangular in outline, with a large, convex median body; the maculae are deeply marked; the posterior marginal border bears 15 short spines.

The pleural lobes of the thoracic segment are long and flat, and deeply impressed by broad and shallow pleural furrows; the pleural spines are long and directed posteriorly and laterally with saw-toothed anterior-lateral borders.

The surface is covered by fine granules; traceable ridges are developed along the cephalic margins.

Remarks. The present species was obtained from a single sample of black, medium-crystalline limestone which yielded about 15 immature and mature cephala, three hypostomata, and a few thoracic segments. The material also contains Olenellus and Salterella. The morphologic features of the present species are close to those of Laudonia bispinata Harrington (1956) and Wanneria ("Laudonia") mexicana prima Lochman (1952),

but it differs from those two forms in that the palpebral lobes are smaller, the marginal furrow is shallower, and the anterior glabella is less expanded. It is interesting to note that the early meraspis most nearly resembles Olenelloides armatus Peach (1894), which was found in west of Ross-Shire, Scotland, in the Lower Cambrian, and studied by Peach (1894) and Walcott (1910). Both forms have a pentagonal to hexagonal cephalon, three pairs of cephalic spines, and no facila sutures; however, the immature forms of L. canadiensis show the pair of palpebral lobes is larger and the skeletal measurements smaller. Undoubtedly these two genera are closely related.

Horizon and Locality. Lower Cambrian. North of Radium, west side of the Columbia River, British Columbia, Canada.

Figured specimens. Holotype, Cranidium, U.C.M. 38726.
Paratype, Cranidia, U.C.M. 38726a-c, g-i.
Hypostomata, U.C.M. 38726e, d.
Thoracic fragment, U.C.M. 38726f.

Laudonia canadiensis, n. sp., ontogeny

Early meraspid stage (Pl. 3, figs. 20,21 and text-fig. 37A). The smallest cephalon varies from 1.2 mm. to 1.7 mm. in length (sag.); the outline is hexagonal, convex, and bears three pairs of cephalic spines. The cylindrical axial lobe is separated into a rounded, convex frontal lobe and four transverse and undifferentiated axial rings; the last axial ring or occipital ring bears a minute median spine. The palpebral lobes are sickle-shaped and extend from the posterior lateral margins of the frontal lobes to the mid-length of the fourth axial ring (tr.).

They are elevated above the fixigenae and delimited by palpebral furrows. The outer fixigenae are broad anterior-laterally, and narrow posterior-laterally; the narrow posterior fixigena is marked by a pair of prominent ridges; the posterior fixigenal ridges extend from the pre-occipital ring to the posterior-lateral corners and are continuous with a pair of spines projecting from the posterior lateral borders. The marginal border is narrow, and convex, and well-delimited by a deep marginal furrow. Three pairs of cephalic spines project outward at the cephalic corners.

The surface of the skeleton is covered by fine granules.

Late meraspid stage (Pl. 3, figs. 25,28-29, and text-fig. 37B). The cephalon is nearly pentagonal in outline, convex, arching forward anteriorly. It ranges from 1.20-2.50 mm. in length. The glabella is cylindrical but expands slightly both anteriorly and posteriorly from the third ring; the frontal lobe is spherical and convex above the outer fixigenae; the second glabellar ring is narrow (sag.) and transverse; the third glabellar ring is triangular with the apex pointing backward; the fourth one is of medium width, convex and arches posteriorly; the glabellar furrows are all steep-sided; the first and the second cross the axis,and the third is separated. The convex occipital ring is wider than the other glabellar rings and defined by a steep-sided occipital furrow; it bears a minute median spine. The palpebral lobe is elevated above the fixigenae, sickle-shaped and divided by palpebral furrow. The outer fixigenae are narrow, gently convex, and slope downward to the deep marginal furrow. The convex marginal border is narrow and bears a pair of cephalic spines anterior-laterally, a pair

laterally, and one pair posterior-laterally; the posterior lateral spines are continuous with a pair of posterior fixigenal ridges which extend to the sides of the pre-occipital ring. The hypostoma is subtriangular in outline, elongate and has a convex median body; the maculae are deep laterally and shallow across the central axis; the posterior lobe is U-shaped, gently convex, and bears 15 dentations along the posterior margin.

The surface is covered by fine granules.

The morphologic changes during the growth stages are as follows: the shape of the cephalon changes from a hexagonal to a pentagonal outline; the anterior cephalic spine becomes shorter and disappears; the glabellar rings change in configuration from stage to stage; the posterior fixigenal borders are expanded laterally (tr.); and the size of the median body of the hypostoma increases while the posterior marginal dentations shorten.

Figured specimens. Early meraspides, U.C.M. 38726a, b.
Late meraspides, U.C.M. 38726d, g-i.

Family Dolichometopidae Walcott, 1916

Genus Ptarmigania Raymond, 1928

Ptarmigania aurita Resser

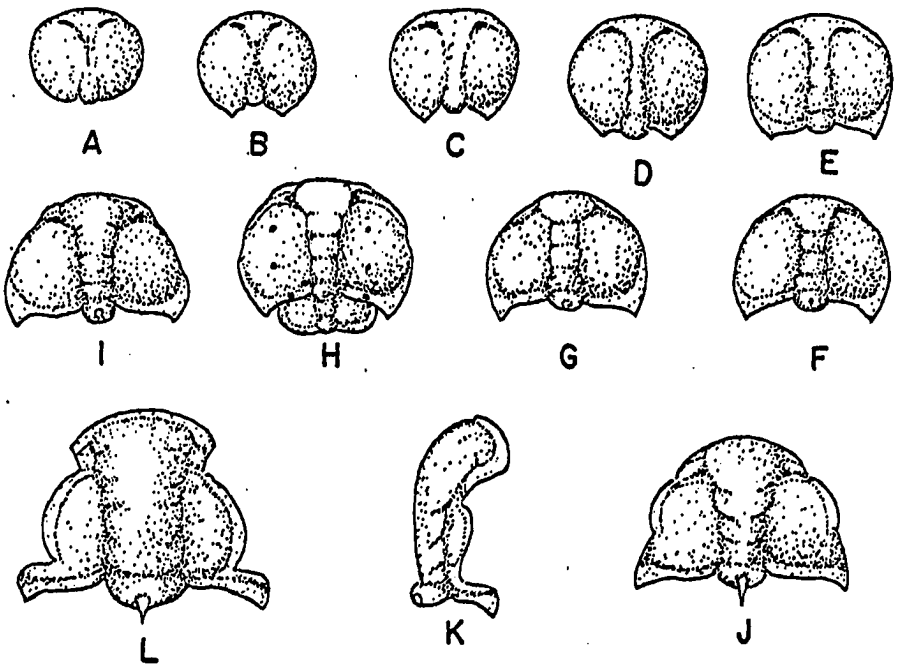
Pl. 4, figs. 1-23 and text-fig. 38

Ptarmigania aurita Resser, C. E., 1939, p. 37, pl. 3, figs. 35,36.

Ptarmigania sp. undetermined, Resser, C. E., 1939, p. 42, pl. 3, fig. 34

Diagnosis. Dolichometopid trilobites with subquadrate glabella expanding anteriorly; large palpebral lobes located far behind the mid-length of glabella (tr.). Fixigenae about half as wide as glabella (between palpebral furrow and dorsal furrow); narrow in front; narrow behind (subequal to width of occipital ring); dorsal furrow distinct; occipital ring bearing a minute, short, median spine. Anterior border very narrow. Librigenae, thoracic segment, and pygidium unknown.

Description. The cranidium is triangular in outline. The subquadrate glabella, which expands slightly anteriorly, is marked by four pairs of glabellar furrows; the anterior pair is shallow and faint and directed anteriorly from the dorsal furrows; the posterior two pairs are deeper, and directed posterior-laterally from the dorsal furrows. The occipital furrow is deep and narrow; the occipital ring is crescentic, convex, arching posteriorly, and bearing a medium-sized median spine. The fixigenae are gently convex, and flattened near the palpebral furrow area, and about one-half as wide as the glabella between the dorsal furrow and the palpebral lobe. The large and narrow palpebral lobes are delimited by palpebral furrows, extending posteriorly from between the first and second glabellar furrows and ending in front of posterior fixigenal furrows; the palpebral ridges are short and prominent.



Text-fig. 38: A growth series of Ptarmigania aurita Resser. A-C, three anaprotaspides, x 40, x 43, x 38; D, a metaprotaspis, x 40; E-G, three paraprotaspides, x 37, x 35, x 33; H, I, two early meraspides, x 28, x 30; J, a late meraspis, x 25; K, L, dorsal and side views of an holaspid cranidium, x 12. (Drawings from photographs.)

Both anterior and posterior fixigenae are rather narrow and convex; the narrow (sag.) posterior lateral borders are about the same width (tr.) as the glabella and are convex above the deep border furrows. The narrow and convex anterior border is adjacent to anterior glabellar margin. The anterior facial suture lines are convergent convex; the posterior ones are almost parallel to the posterior-lateral borders. The surface is finely granulated.

The librigenae, hypostoma, thoracic segments, and pygidium are unknown.

Remarks. This species is represented by more than 55 immature and mature specimens. All were prepared from a few small pieces of dark grey, medium-cyrstalline limestone. The samples also include both early instars and adults of Elrathina, Alokistocare and Pagetia. The immature forms are different from those of ptychopariids in having a rather narrow axial lobe, and impossible to mistake for those of Pagetia since the forms are so characteristic (see p. 162 and pl. 1, fig. 23-26).

The complete skeleton of the type of Ptarmigania ("Bathyuriscus") rossensis (Walcott) (type of genus) (1917) shows a cephalon with long genal spines, 9 thoracic segments, and a pygidium with a broad marginal border and a pair of anterior-lateral spines. Resser (1939) assigned to this genus a few species based on disassociated body parts. It is therefore difficult to evaluate his assignments. It is likely, as pointed out by Rasetti (1951, p. 169), that in most corynexochid trilobites, secure generic and specific determinations can only be based on essentially complete specimens which show the number of thoracic segments and the shape of the pygidium. It is obviously untrustworthy

to attribute any single cranidium to species or genus within the group. In the absence of any closely similarly librigena which can be securely correlated with the present cranidium and with no potentially assignable pygidia known, Resser's unsatisfactory assignment is perforce here adopted.

Horizon and Locality. Middle Cambrian, Elrathina-Bathyuriscus zone. Santaqiun Canyon, Northeast side of road, Wasatch Mts., Utah.

Figured specimens. Cranidium, U.C.M. 38727.

Cranidia, U.C.M. 38727a-u.

Ptarmigania aurita Resser, ontogeny

Anaprotaspid stage (Pl. 4, figs. 1-5 and text-fig. 38A-C). The shield is spherical to slightly transverse, convex, without distinct dorsal furrows, and ranges from 0.28-0.35 mm. in length (sag.). The axial region is slightly elevated with a faint longitudinal fissure along the axis. No axial rings or furrows are present, and the frontal lobe is poorly defined; the anterior pits are transversely elongate and distinctly impressed on the sides of the frontal lobe; a pair of short eye-brow-shaped ridges extend laterally from the anterior lateral margin of the frontal lobe. A terminal tubercle is slightly elevated on the edge of the posterior median margin of the shield. The posterior lateral margin has a pair of short, broad spines directed backward.

The surface is covered by fine granules.

Metaprotaspid stage (Pl. 4, figs. 6,7 and text-fig. 38D). The shield is rounded, convex, with distinctly divided axial and pleural lobes, it is approximately 0.40 mm. long (sag.). Both ends of the axial

lobe expand from the second axial ring; both axial rings and furrows are distinctly defined; the frontal lobe is rounded, triangular, with a pair of supercilioid ridges directed laterally and posteriorly from the anterior lateral margin; the anterior pits are elongate and deeply marked; the second axial ring is small, narrow and elongate; the third and fourth are oval and larger, rounded, and highly convex. The pleural lobe is convex anteriorly and gently sloping downward posterior-laterally towards the margin. A pair of short, broad spines project backward from the posterior-lateral margin. The protopygidium is unknown. The surface is finely granulose.

This stage differs from the previous one in having the shield distinctly divided into axial and pleural lobes, and the axial lobe segmented into five distinct rings.

Paraprotaspid stage (Pl. 4, figs. 8-13, 15 and text-fig. 38E-G). The crandium, which is trapezoidal to subtrapezoidal in outline, bears well developed axial and pleural lobes and ranges from 0.45-0.55 mm. in length (sag.). The axial lobe expands both anteriorly and posteriorly from the second axial ring; the frontal lobe is triangular, convex, and arching forward with a pair of eye-ridges; the anterior pits are distinct; the second ring is narrowing elongate, the third and fourth ones are larger, rounded to roundly transverse; the occipital ring is smaller and transverse. The dorsal furrow is deeply impressed. The fixigenae are convex, very broad, about three times as wide as the glabella (tr. at mid-length). The supercilioid ridges are prominently elevated, situated behind the frontal pits, and directed posterior-laterally to be connected with the narrow palpebral lobes. The posterior lateral

furrows are distinct. The posterior-lateral borders are narrow and have a pair of short spines projecting backward from their mid-line (tr.). The anterior branches of the facial sutures are convergent and the posterior branches are divergent and their course is either sinous or straight. The surface is covered by fine granules.

The characteristics of this stage are the trapezoidal crandium, the dorsal facial sutures and the appearance of the protopygidium.

Early meraspid stage (Pl. 4, figs. 14, 16-18 and text-fig. 38H, I). The cranidium is trapezoidal in outline, moderately convex, and varies from 0.55 to 0.65 mm. long (sag.). The glabella is strongly expanded forward, with distinct anterior pits on the sides of the first glabellar segment; the glabellar furrows are faint but steep-sided. The dorsal furrow is deep; the convex occipital ring bears a minute median spine. The fixigenae are broadly triangular, convex, less than twice as wide as the glabella (tr.); the eye ridges are prominently elevated and directed posterior-laterally from the sides of the anterior pits; the palpebral lobe is narrow and long; the posterior lateral border is narrow (sag.) and about twice as wide as the occipital ring (tr.). The surface is finely granulose, and three pairs of prominent nodes occur on the fixigenae.

In comparison to previous stages, the specimens of this stage have a marked forward expansion of the glabella and narrow fixigenae.

Late meraspid stage (Pl. 4, figs. 19, 20 and text-fig. 38J). The convex cranidium is about 0.80-1.00 mm. long (sag.). The important characteristics of this stage are the first appearance of the anterior border; the lengthening of the palpebral lobes, which here extend

posteriorly to the posterior-lateral border; and disappearance of the anterior pits. The specimens of the meraspid stage are differentiated from those of the holaspid stage in having wider fixigenae and the palpebral lobes situated at the mid-length of the glabella (tr.).

Figured specimens. Anaprotaspides, U.C.M. 38727a-e.

Metaportaspides, U.C.M. 38727f, g.

Paraprotaspides, U.C.M. 38727h-m, o.

Early meraspides, U.C.M. 38727n, p-r.

Late meraspides, U.C.M. 38727s, t.

Family Anomocaridae Poulsen, 1927

Genus Glyphaspis Poulsen, 1927

Glyphaspis cf. parkensis Rasetti

Pl. 5, figs. 1-30 and text-fig. 39

Glyphaspis parkensis Rasetti, F., 1951, p. 224, pl. 34, figs. 5-7;

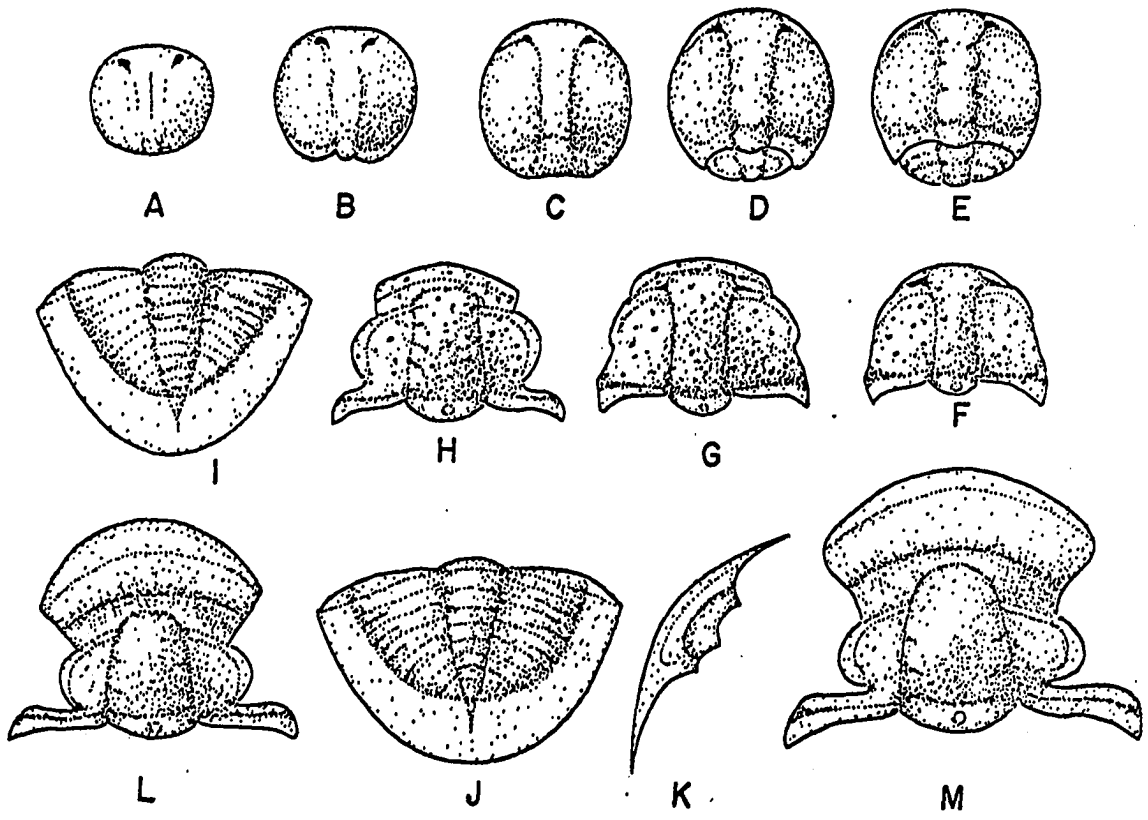
Poulsen, V., 1964, p. 51, pl. 3, figs. 8,9.

Diagnosis. Skeleton very similar to that of Anomocare: cranidium quadrate in outline, with very wide and concave frontal brim. Fixigenae medium-narrow. Palpebral lobe long, sickle-shaped, and located behind the mid-line of glabella (tr.). Librigenae elongate with along genal spine. Pygidium large with broad, usually concave, marginal border. Axial lobe conical and backwardly tapering, divided into 7 or 8 axial rings and a small posterior terminal portion.

Glyphaspis cf. parkensis Rasetti, male?

Pl. 5, figs. 15-18, 22, 27 and text-figs. 39I, L.

Description. The skeleton is large, convex, with semi-circular cephalon and pygidium. The cranidium is quadrate in outline. The glabella is conical with a rounded anterior margin and rather shallow, broad glabellar furrows. The dorsal furrow is shallow but well defined. The shallow occipital furrow curves slightly forward at the mid-line (sag.). The frontal brim is very indistinctly separated into an anterior border and preglabellar field by a furrow; the anterior border is broad and concave, and marked laterally with very delicate furrows; the anterior furrow is faint but well defined; the preglabellar field is narrow, i.e., the anterior border is more than three times as wide as the



Text-fig. 39: Glyphaspis cf. parkensis Rasetti. A,B, two anaprotaspides, x 53; C, a metaprotaspis, x 45; D,E, two paraprotaspides, x 40, x 30; F,G, two early meraspides, x 26, x 24; H, a late meraspis, x 20; I, a "male" pygidium, x 1.7; J, a "female" pygidium, x 1.7; K, librigena, x 10; L, a "male" cranidium, x 1.6; M, a "female" cranidium, x 7. (Drawings made from photographs.)

preglabellar field. The fixigenae are about one-half the width of the glabella; the palpebral lobes are crescentic, more than half as long as the glabella, sickle-shaped and located behind the mid-line of the glabella (tr.); eye-ridges are distinctly marked; the posterior fixigenae are narrow and marked by narrow distinct border furrows; the posterior lateral borders are narrow and slender. The anterior facial suture is considerably divergent and cuts the anterior border roundly; the posterior facial suture is almost parallel to the posterior lateral border.

The librigenae are elongate and have long genal spines; the librigenal lateral border is very broad, and flat or slightly concave, with a very faint furrow along the inner marginal border; the lateral furrow is faint but clearly recognizable; the ocular platform is narrow and gently convex; the genal spine is long and arcuate, with a broad base that tapers gradually to the tip.

The pygidium is elongate semi-ovate in outline, with a convex axial lobe and broad concave border. The axial lobe is slenderly conical, broad anteriorly and tapering posteriorly to the inner marginal furrow; 6 or 7 small axial rings and a small posterior portion are seen; the ring furrows are shallow and they are slightly curving anteriorly at the central axis. The pleural lobes are convex, gently sloping downward from the dorsal furrow to the inner marginal furrow, and distinctly divided into 6 or 7 pleural furrows.

The surface of the skelton is covered by fine granules; radial ridges are marked on the preglabellar field and ocular platform of the librigenae, the outer of the cephalic margins are surrounded by fine

wrinles.

Figured specimens. Cranidia, U.C.M. 38728o-q.

Librigena, U.C.M. 38728S.

Pygidium, U.C.M. 387284.

Hypostoma, U.C.M. 38728r.

Glyphaspis cf. *parkensis* Rasetti, female?

Pl. 5, figs. 19,20,26,28-30 and text-fig. 39J, M.

The characteristics of what is presumed to be the females differ from those of the presumed males in that the female body is remarkably larger than the male and has a narrower and less conves anterior border; the glabella is narrow and longer, and the pygidium has a rounded outline.

Remarks. This species is represented by 20 mature and 60 immature specimens, all are prepared from a few small pieces of dark-grey oölitic, medium-crystalline limestone. The features of the present species conform to Rasetti's description, but unfortunately the holotype and the paratypes of *G. parkensis* are all slightly deformed; moreover, the holotype was a shale specimen, hence its characteristics are not exactly identical with those of the limestone specimens here studied. The main portion of the preglabellar field of the paratype (U.S.N.M. 116286a) is slightly wider and that of the holotype (U.S.N.M. 116825) and was exfoliated. Therefore, if diagenetic factors are considered, the present material may present the original shape and convexity. The specimens identified as this form which were found in northwestern Greenland by Poulsen (1964) show a narrower frontal brim, and narrower

pygidial marginal border than both Rasetti's and present materials. Poulsen's material may represent a variety of this species. The sexual ratio of the present species is 125.

Horizon and Locality. Meagher Formation, Middle Cambrian, Bathyuriscus-Elrathina zone. West side of South Boulder Creek, West Madison County, Montana.

Figured specimens. Cranidium, U.C.M. 38728

Pygidia, U.C.M. 38728w, x, z, r.

Glyphaspis cf. parkensis Rasetti, ontogeny

Anaprotaspid stage (Pl. 5, figs. 1-3 and text-fig. 39A, B). The convex shield is rounded to subrounded in outline, with a rather narrow shield margin and varies from 0.25 to 0.30 mm. in length (sag.). The axial and pleural lobes are undivided; a narrow but traceable longitudinal axial fissure is well-defined on small shield but absent on larger ones. The frontal lobe is delimited by two distinct anterior pits; a pair of short supercilioid ridges extend from the anterior-lateral margin of the frontal lobe. The hind margin of the shield bears a rounded to elongate median tubercle or occipital ring. A pair of short, broad-based marginal spines project from the posterior-lateral margin of the shield. The surface is covered by fine granules. A narrow marginal border surrounds the shield.

Metaprotaspid stage (Pl. 5, figs. 4, 5 and text-fig. 39C). The shield is subrounded in outline, convex and about 0.40-0.50 mm. in length (sag.), with well defined axial and pleural lobes. No axial ring or glabellar furrows are seen. The anterior pits are deeply impressed;

the frontal lobe is broad and convex, with a pair of supercilioid ridges extending posterior-laterally along the front margin. The axial lobe is cylindrical but with a broadly expanded frontal lobe; the posterior axial lobe is distinguished by a prominent tubercle. The lateral lobe is convex and twice as wide as the axial lobe. The posterior margin of the shield arches to the axial lobe, with flat, narrow, and unsegmented marginal fringe. The marginal border is present along most the posterior-lateral shield margin. The surface is covered by fine granules.

The important features of this stage are: the axis and the pleural lobes are well differentiated; the central axial fissure has disappeared; and the posterior shield margin bears a narrow, flat fringe.

Paraprotaspid stage (Pl. 5, figs. 6, 7 and text-fig. 39 D, E). The shield is composed of a cephalon and a protopygidium; it is subspherical in outline and convex, with the length about 0.55-0.75 mm. (sag.). The axial and pleural lobes are distinctly separated by dorsal furrows. The glabella is cylindrical with a slightly expanded frontal lobe, four faint glabellar rings and a rather prominently elevated occipital ring; the glabellar furrows are steeply sided and extend across the axis. The anterior pits are shallower than those of the previous stage, but clearly recognizable. The pleural lobes or fixigenae are convex and about one and one-half the width of the glabella; the posterior-lateral border are backwardly projected. The transversely subtriangular protopygidium is composed of 1 or 2 segments. The surface is finely granulose.

This stage differs from the previous one in that the shield is composed of a clearly differentiated protopygidium and cephalon; the

pleural lobes are narrower, and the frontal pits are shallower; the palpebral ridges are prominently elevated.

Early meraspid stage (Pl. 5, figs. 8-11, 23-24 and text-fig. 39F,G). The convex crandium is triangular in outline and about 0.60-0.80 mm. in length (sag.). The glabella is broadly cylindrical with indistinct glabellar furrows. The dorsal furrows are narrow and deeply impressed. The anterior border is narrow and arches forward. The occipital ring is convex, and bears a small median tubercle. The fixigenae are about the same width as the glabella and are broadly triangular with a distinct posterior lateral border; the eye ridges are prominently elevated; the palpebral lobe is large and situated in front of the med-line of the glabella (tr.). The pygidium is transversely oval and divided into 2 or 3 segments by distinct furrows (fig. 23, 24). The surface is covered with large granules.

This stage is characterized by the appearance of the anterior border; the fixigenae are about the same width as the glabella, which here becomes cylindrical. The pygidium is separated from the cephalon by a few thoracic segments.

Late meraspid stage (Pl. 5, figs. 12-14, 25 and text-fig. 39H). The cranidium is trapezoidal in quadrangular in outline, moderately convex, and about 1.00 to 1.80 mm. in length (sag.). The glabella is truncate-conical with broad, shallowly impressed glabellar furrows. The occipital ring is crescentic, convex, and has a small median tubercle. The preglabellar field first appears in this stage and is separated by the anterior furrow from the border; the anterior brim varies in width, narrower on smaller forms and broader and flat on

larger ones. The fixigenae are about one-half the width of the glabella; the palpebral lobe is crescentic, and located at the mid-line of the glabella (tr.). The pygidium is oval or subtriangular with 6-7 segments; the marginal border is narrow. The surface is covered by coarse granules in smaller specimens, but finer in the larger forms.

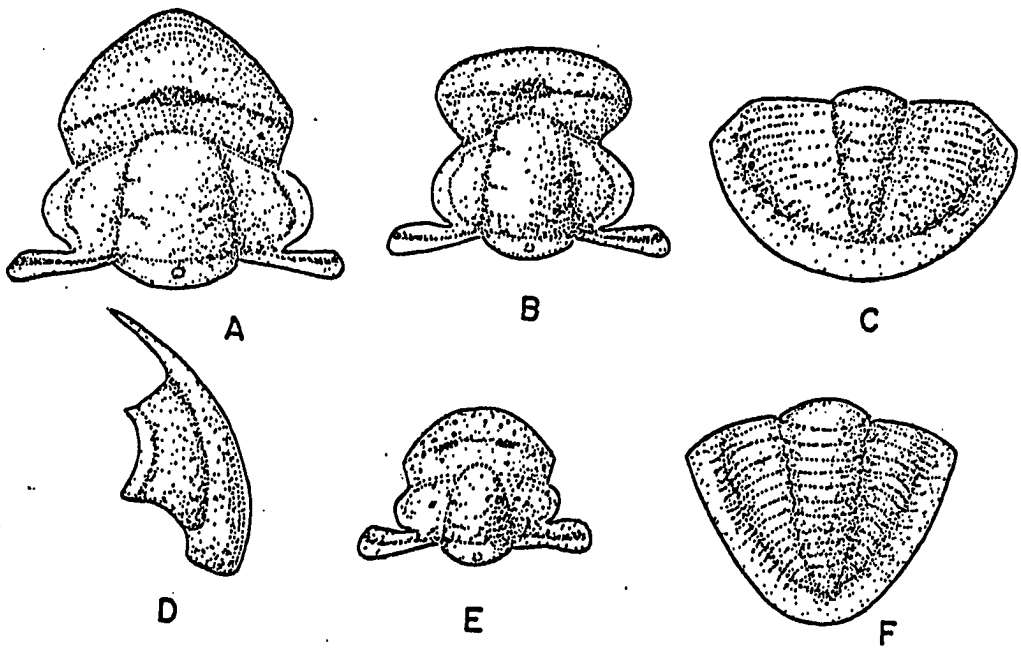
The most distinctive characteristics of this stage are: cranidium bears a clearly defined preglabellar field; the glabella becomes truncate-conical, and the palpebral lobes are located at the mid-line of the glabella (tr.). This stage differs from the holaspid stage in that the glabella of the meraspis is less rounded at the frontal margin; the anterior margin has no border furrow; and the palpebral lobe of the holaspis is located slightly behind the mid-length of the glabella.

Figured specimens. Anaprotaspides, U.C.M. 38728a-c.
Metaprotaspides, U.C.M. 38728d, e.
Paraprotaspides, U.C.M. 38728f, g.
Early meraspides, U.C.M. 38728h-k, t, u.
Late meraspides, U.C.M. 38728l-n, v.

Genus Iohomia, n. gen.

Diagnosis. Cranidium subquadrate in outline; glabella conical; glabellar furrows faint; dorsal furrow deep and board; preglabellar field moderately narrow; anterior furrow broad, well defined, bearing a median pit; anterior border broad and flat. Fixigenae narrow, convex above dorsal furrow; palpebral lobes large and sickle-shaped, situated posterior to the mid-length of the glabella; posterior fixigenae rather narrow; librigenae with broad, flat lateral borders; genal spine unknown. Pygidium rounded to subtriangular in outline, highly convex along the axis; possibly divided into more than ten segments; marginal border rather broad and flat.

Description. The cranidium is subquadrate, elongate, moderately convex, with a broad flat frontal brim. The glabella is conical, rounded in front, and marked with very shallow glabellar furrows. The dorsal furrow is deep and broad, but shallow along the anterior glabellar margin. The occipital ring, which is broad centrally, and narrower laterally, bears a minute median tubercle. The occipital furrow is distinct, shallow across the central axis, and steep-sided. The preglabellar field is narrow and slopes downward to the shallow anterior furrow, which arches forward to a transverse, ovate median pit. The anterior border is broad and flat, subtriangular to crescentic. The fixigenae are narrow, about one-third as wide as the glabella and steeply convex above the dorsal furrow. The larger palpebral lobes are sickle-shaped, and located behind the mid-line of the glabella. The prominent palpebral ridges are obliquely directed anterior-midially from the anterior palpebral lobes to points immediately behind the



Text-fig. 40: Iohomia sickia, n. gen. et sp. A, "male" cranidium, 2.5; B, "female" cranidium, x 4.3; C, a "female" pygidium, x 2.2; D, librigena, x 5.4; E, a late meraspid cranidium, x 10; F, a "male" pygidium, x 3. (Schematic drawings from photographs.)

anterior-lateral corners of the glabella. The narrow posterior fixigenae are deflexed steeply from the posterior palpebral lobes to the deep and broad border furrow, and are larger laterally (tr.) than the occipital ring. The anterior facial sutures are strongly convergently convex, and the posterior ones are divergently sinuous, and nearly transverse.

The librigenae may lack genal spines. The ocular ring is large and located above the ocular platform. The lateral border is broad and flat, or slightly concave, anteriorly, and delimited by a broad, shallow lateral furrow.

The pygidium is elongate-subtriangular in outline and convex along the axis. The axial lobe is slenderly conical, tapering posteriorly, and ending before reaching the pygidial margin. It is divided into at least ten narrow axial rings and a small subtriangular terminal portion. The pleural lobes are more than one-half times as wide as the axis and marked by very shallow pleural furrows which extend into the broad, flat marginal border.

The skeletal surface is covered by fine granules; radial ridges are marked on the preflabellar field, and wrinkles occur along the cephalic margin.

Remarks. The present genus is very similar to Anomocare and Glyphaspis, but it differs in having a cranidium bearing an anterior median pit, narrower glabella, and subtriangular anterior border. The pygidium is highly convex along the axial lobe. The general appearance indicates close relationship to other genera in the family Anomocaridae.

Type species. Iohomia sickia, n. gen. et sp.

Iohomia sickia, n. gen. et sp., male ?

Pl. 6, figs. 15, 18, 19, 21, 22, 25, 26, and text-fig. 40A, D, F. The cranidium is triangular in outline with broadly subtriangular anterior border; glabella conical, broad and short; anterior furrow occupied by a transverse, ovate median pit. Librigenae without genal spines. Pygidium elongate, subtriangular, and highly convex along the axial lobe.

Holotype. Cranidium, U.C.M. 38737.

Paratypes. Cranidium, U.C.M. 38737i.

Pygidia, U.C.M. 38737c, f.

Librigena, U.C.M. 38737 e.

Meraspis, U.C.M. 38737a.

Iohomia sickia, n. gen. et sp., female ?

Pl. 6, figs. 17, 20, 23, 24 and text-fig. 40B, C.

The cranidium is subquadrate in outline, with a narrow transverse, crescentic anterior border; the glabella is slightly narrower and longer than that of the male form. The pygidium is semi-circular or semi-oval in outline and uniformly convex.

Remarks. This species is represented by more than 30 specimens; the smallest form is about 1.5 mm. in length (sag.) and represents the meraspid stage; the largest crandium is about 15.0 mm. and the largest pygidium 14.0 mm. in length (sag.). All of the specimens were prepared from a few small pieces of dark-grey, medium-crystalline limestone.

Horizon and Locality. Meagher Formation, Bathyuriscus-Elrathina zone, Middle Cambrian. West side of South Boulder Creek, West Madison County, Montana.

Figured specimens. Paratypes.

Cranidia, U.C.M. 38737g, h.

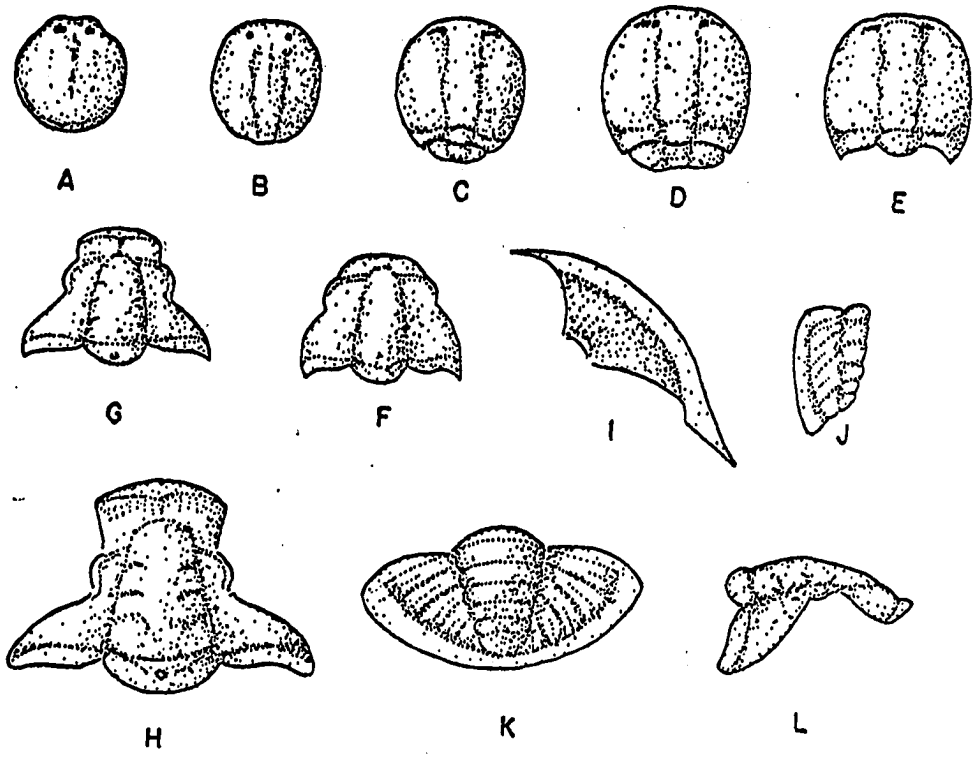
Pygidia, U. C. M. 38737b, d.

Family Parabolinoididae Lochman, 1956

Genus Apomodocia, n. gen.

Diagnosis. Cranidium triangular in outline, elongate, moderately convex. Glabella slenderly conical with three pairs of faint glabellar furrows. Dorsal furrow narrow and shallow. Occipital ring crescentic, convex, bearing a minute median tubercle. Anterior furrow with median notch. Anterior border narrow and convex. Fixigenae narrow about one-third as wide as glabella. Palebral lobe small, located in front of the mid-line of glabella (tr.). Fixigenae broad, posteriorly subtriangular, with the border the same width as the occipital ring. Librigenae crescentic, elongate with a short genal spine. Hypostoma subquadrate and bearing a broad median body. Convex pygidium, subtriangular in outline, consisting of 3 or 4 segments, with a narrow marginal border.

Description. The cranidium is triangular in outline, elongate, and moderately convex. The glabella is a slender cone, tapering forward with a rounded anterior margin; three pairs of very faint glabellar furrows are present; the first pair is short and located in front of the transverse line of the palpebral lobes; the second pair is of medium length and directed posteriorly from behind the transverse line of the palpebral lobes; the third pair of glabellar furrows is longer and deeper than the preceding pairs. The dorsal furrow is narrow and deeply defined. The occipital furrow is deep and steep-sided laterally but shallow across the central axis. The occipital ring is broadly convex, crescentic and bears a minute median tubercle. The anterior brim extends one-third the length of the glabella and is



Text-fig. 41: A growth series of Apomodocia conica, n. gen. et sp. A, anaprotaspis, x 43; B, metaprotaspis, x 38; C-E, paraprotaspides, x 36, x 36, x 36; F, an early meraspis, x 40; G, a late meraspis, x 17; H.L, dorsal and side views of an holaspid cranidium, x 5.4; I, a ligrigena, x 4.3; J,K, top and side views of a pygidium, x 3.6. (Schematic drawings made from photographs.)

gently convex. The anterior furrow is shallow, broad and distinctly defined with a median notch directed towards the anterior margin of the preglabellar field; the convex anterior border is of medium width. The fixigenae are with slightly expressed palpebral lobes, which are one-third as wide as the glabella (tr.); the narrow palpebral lobes are small and located in front of the mid-line of the glabella; the palpebral furrows are faint. The posterior fixigenae are subtriangular in outline and marked by broad, deeply impressed border furrows. The anterior branches of the facial sutures are straight and diverge anteriorly; the posterior branches are strongly divergent posteriorly and are gently sinuous.

The librigenae are crescentic with short posterior lateral genal spines. The ocular platform is moderately narrow. The lateral border is medium - arrow, slightly convex, and distinctly delimited by a shallow, broad lateral furrow.

The moderately convex pygidium is transversely subtriangular to ovate in outline. The axial lobe is conical, tapering posteriorly and marked by 3 or 4 axial rings and a semi-circular posterior portion. The dorsal furrow is distinct. The pleural lobes are gently convex, with three pairs of distinct segments; the pleural furrows and the interpleural grooves are distinctly defined. The marginal border is of medium width, narrowing slightly posteriorly, and moderately convex.

The surface is covered by fine granules, and radial ridges are marked on the preglabellar field and the ocular platforms of the librigenae.

Remarks. This genus differs from Modocia Walcott (1924) by its

triangular cranidium of low convexity; the glabella of Apomodocia is longer and narrower; the dorsal furrow is shallow; the preglabellar field is wider and fixigenae are narrower; the librigenae have shorter genal spines; the pygidium lacks marginal spines. The Modocia skeleton is covered by very large granules whereas that of Apomodocia is smooth or covered with fine granules.

The general features of Apomodocia are very similar to those of Parabolinoides Frederickson (1949), and Maustonia Raasch (in Lochman, C. B., 1950), but Apomodocia shows a slightly more slender glabella, narrower anterior border, shorter genal spines, and a pygidium lacking marginal spines. On the other hand, the location of the palpebral lobes, the narrow fixigenae, the small ocular ring, the shallow dorsal furrow, and the posteriorly broad fixigenae are similar in all these genera. Like there, Apomodocia should be a member of family Parabolinoididae.

Type species. Apomodocia conica, n. gen. et sp.

Apomodocia conica, n. gen. et sp.

Pl. 3, figs. 1-19 and text-fig. 41.

Armonia late (Howell and Duncan), Lochman, C. B. and Duncan, D., 1944, p. 122, pl. 15, figs. 30-36 only (not figs. 29, 37); Lochman, C. B., 1950, p. 346, pl. 51, figs. 11-15 only (not fig. 10, 12).

Remarks. This species is represented by more than 50 immature and mature specimens, all prepared from a few pieces of light-brown, medium-coarse crystalline limestone. The material contains also both larval and adult forms of Cedarina cordillerae (Howell and Duncan). The larvae of A. conica differ from those of C. cordillerae by their

narrower axial lobes and absence of occipital spines.

The present genus and species present certain taxonomic problems. The holotype (M.S.U.M. T1616) of Armonia lata (Howell and Duncan) was originally assigned as Perioura lata Howell and Duncan, (1938). After a re-examination of the holotype of A. lata, Lochman and Duncan (1944) removed the original assignment as a new species of Armonia lata and subsequently assigned several specimens to this species. Lochman (1959, Treatise, Part O, p. 306) synonymized Armonia Walcott (1924) with Modocia Walcott (1924) without giving any reasons. The writer had an opportunity to carefully study the original materials of the type species of Modocia, Armonia, and Perioura with Dr. Lochman at the New Mexico Institute of Mining and Technology a few years ago. It is unfortunate that the holotype of A. elongata Walcott (1924) (U.S.N.M. 62811) is an internal mold of an imperfect cranidium and that of Perioura ("Amonia") lata (M.S.U.M. T 1616) is a cranidium from well compacted shale. Thus, they could not be exactly compared, but taking into account the preservation, the general shape of the cranidium, the position of the palpebral lobes, etc., it was our conclusion that the types of Armonia elongata (Walcott) and Perioura ("Armonia") lata Howell and Duncan should belong to the genus Modocia, and that the subsequent assignments by Lochman and Duncan (1944) and Lochman (1950) pertain to other genera.

Lochman's Armonia lata (1950, pl. 51, fig. 10, 12 only) may belong to the genus Blountia. However, this is speculative because of the poor preservation of the material.

Horizon and Locality. Upper Cambrian, Cedaria zone. Princeton,

Wasatch Mts., Utah.

Figured specimens. Holotype, Cranidium, U.C.M. 38725

Paratype, Cranidia, U.C.M. 38725a-p.

Apomodocia conica, n. gen. et sp., onotgeny

Anaprotaspid stage (Pl. 3, fig. 1 and text-fig. 41A). The shield is rounded in outline, moderately convex, and approximately 0.30 mm. in length (sag.). The axial and pleural lobes are not well differentiated except for an elongate median fissure, which extends from the anterior margin to the mid-length of the shield. A pair of anterior pits, which suggest the instars' orientation, are distinctly marked on the anterior lateral margin of the shield. The surface is covered by fine granules.

Metaprotaspid stage (Pl. 3, figs. 2, 3 and text-fig. 41B). The shield is subrounded, moderately convex, and about 0.30-0.40 mm. in length (sag.). The axial and pleural lobes are distinctly separated; the dorsal furrows are rather faint and parallel; no axial ring or ring furrows occur but a small terminal tubercle is situated at the posterior margin of the shield. The anterior pits are rounded and distinctly marked. A pair of supercilioid ridges are directed laterally and posteriorly from the anterior lateral margin of the frontal lobe. The posterior tubercle is rounded, transverse, and faintly separated from the axial lobe by a furrow. The convex pleural lobes are broader than axis; the marginal border is rounded and depressed.

The instars of this stage are characterized by the well developed

axial and pleural lobes; the longitudinal fissure is absent.

Paraprotaspid stage (Pl. 3, figs. 4-8, and text-fig. 41C-E). The shield, which is distinctly divided into cephalon and protopygidium, is subspherical and about 0.45 to 0.50 mm. in total length (sag.). The axial lobe is cylindrical and has distinctly defined dorsal furrows. The anterior pits are rounded and distinctly marked; the eye-brow-like ridge taper posterior-laterally from the anterior lateral frontal lobe. The occipital ring is transverse, oval, convex, and defined by the occipital furrow. The convex pleural lobes are about one and a half times as wide as the glabella and have posterior borders terminating in a pair of posteriorly directed spines. The protopygidium is transversely ovate and composed of one or two segments; the ring and pleural furrows are sharply defined. No marginal spines are observed. The surface of the skeleton is covered by fine granules.

This stage is characterized by a well developed cephalon and protopygidium.

Early meraspid stage (Pl. 3, figs. 9, 10 and text-fig. 41F). The cranidium is convex, trapezoidal in outline, and about 0.45 to 0.70 mm. in length (sag.). The glabella is slenderly conical without distinct glabellar furrows; the dorsal furrow is narrow and deeply impressed; the occipital ring is broadly convex and defined by the occipital furrow. A narrow and forward-arching anterior border is present. The convex fixigenae are about the same width as the glabella and have a pair of prominent palpebral ridges, which are directed laterally from the anterior lateral sides of the glabella.

The small palpebral lobes are located in the anterior quarter of the cranidium. The posterior fixigenae are broad; the posterior lateral borders are narrow, separated by wide and deeply impressed furrows. The anterior branches of the facial sutures are convergent and the posterior branches are transverse, and divergent immediately from behind the palpebral lobe. The surface is finely granulose.

The skeletons of this stage differ from the skeletons of the previous ones by their triangular to trapezoidal crandium, slender glabella, absence of anterior pits, and narrower fixigenae.

Late meraspid stage (Pl. 3, figs. 11, and text-fig. 41G). The cranidium is triangular in outline, convex, and about 1.00 mm. long (sag.). The glabella is slenderly conical with three pairs of short glabellar furrows; the dorsal furrow is deeply defined; the occipital ring is broadly convex and bears a tiny median tubercle. The preglabellar field is narrow and convex; the anterior furrow is faint but has a median notch directed to the preglabellar field; the anterior border is very narrow. The fixigenae are about one-half as wide as the glabella and bear a pair of pronounced palpebral lobes; the posterior fixigenae are broadly triangular, convex, and are deflected laterally. The surface is covered by fine granules.

This stage is characterized by the appearance of the preglabellar field, the anterior furrow with a median notch towards the anterior glabellar margin, and the narrower fixigenae.

Figured specimens. Anaprotaspis, U.C.M. 38725a

Metaprotaspides, U.C.M. 38725b, c.

Paraprotaspides, U.C.M. 38725d-h.

Early meraspides, U.C.M. 38725i, j.

Late meraspis, U.C.M. 38725k.

Family Raymondinidae Clark, 1924

Genus Cedarina Lochman, 1940

Cedarina cordillerae (Howell and Duncan)

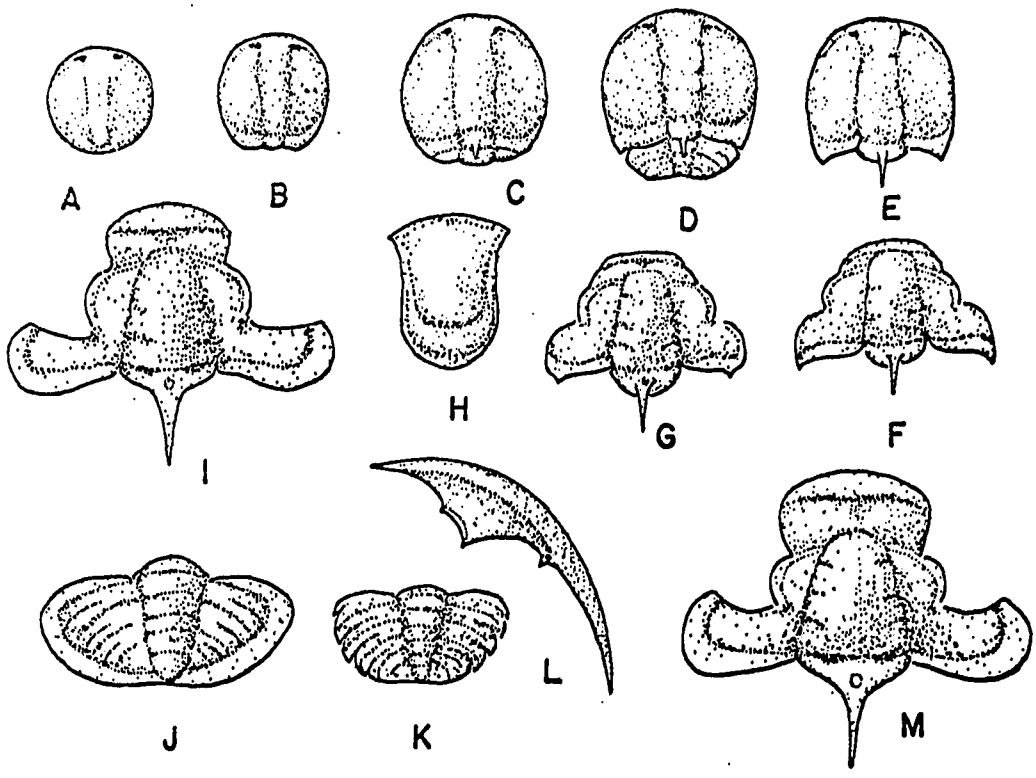
Pl. 7, figs. 1-29 and text-fig. 42.

Piemontia cordilleare Howell, B. F., and Duncan, D., 1939, p. 9, pl. 1, fig. 4.

Cedarina cordillerae (Howell and Duncan), Lochman, C. B., and Duncan, D., 1944, p. 89, pl. 17, figs. 1-10, and Lochman, C. B., 1950, p. 347, pl. 50, figs. 20, 21.

Diagnosis. Conical glabella having three pairs of faint, broad glabellar furrows. Occipital furrow steep-sided and deep. Occipital ring elevated with a large posteriorly directed median spine. Dorsal furrow distinct. Preglabellar field about one-third as long as glabella. Anterior border slightly narrower than preglabellar field. Fixigenae narrow, less than one-half the width (tr.) of the glabella. Palpebral lobes small, located in front of the mid-length of the glabella. Posterior lateral fixigenae broad laterally with border furrows curving forward before reaching lateral margin. Librigenae with long spines and strongly arched genal angles. Hypostoma subquadrate and bearing a strongly convex median body. Pygidium semi-circular; 4 or 5 fused segments, with a flat, narrow marginal border.

Description. The elongate triangular cranidium has cedarid form facial sutures. The conical glabella is rounded anteriorly and bear three pairs of faint glabellar furrows. The dorsal furrows are narrow and deeply impressed. The occipital furrow is shallow but steep-sided. The occipital ring is medium width and bears a small median node and



Text-fig. 42: Cedarina cordillerae (Howell and Duncan). A, anaprotaspis, x 52; B, metaprotaspis, x 40; C,D,E, three paraprotaspides, x 42, x 35, x 36; F, an early meraspis, x 26; G, a late meraspis, x 19; H, hypostoma, x 8; I, a "female" cranidium, x 6; J,K, an adult and a juvenive pygidium, x 6.3, x 26; L, a librigena, x 2.7; M, "male" cranidium, x 4.2. (Drawing made from photographs.)

a long posteriorly directed occipital spine. The preglabellar field is about one-third as long as the glabella, and gently slopes downward to the broad anterior furrow. The anterior furrow arches forward but has a posteriorly directed median notch. The anterior border is broad and slightly convex. The flat to convex fixigenae are narrow and less than one-half as wide as the glabella. The small palpebral lobes lack distinct palpebral furrows and are located anteriorly from the mid-line of the glabella (tr.). The broad palpebral ridges curve posterior-laterally from the anterior-lateral edge of the glabella. The posterior margina of the fixigenae are broad. The wide posterior lateral furrows are shallow, but well-defined. The posterior borders are broad, about the same width as the occipital ring (tr.), and arch forward before reaching the lateral margins. The anterior facial sutures are convergently convex, and the posterior ones are divergently transverse.

The elongate librigenae are narrow with a narrow, slightly convex ocular platform. The marginal furrow is narrow and well-defined; the marginal border is of medium width, convex, with a long, large genal spine.

The hypostoma is subquadrate with a rounded posterior margin; its median body is convex. The moderately convex posterior lobe is distinctly separated from the median body by a shallow, broad macular furrow.

The pygidium is narrowly transverse, its axial lobe is conical, tapering slightly posteriorly and divided into 3 or 4 axial rings and a terminal portion; the pleural lobes are almost flat, narrower than the axis, with three broad pleural segments. The marginal border is

of medium width, flat, and lacking a marginal spine.

The outer surface is covered by fine granules; radial ridges are marked on the preglabellar field and ocular platforms; faint wrinkles are present along the skeletal margins. The inner surface is minutely punctate.

Remarks. This species is represented by 75 immature and mature specimens. The adult crandia can be separated into two groups: one with a narrower and longer glabella and the other with a broader and shorter one. These characteristics might indicate sexual dimorphism, but Lochman (1944) stated that there is present still another form, Cedarina prima Lochman, without an occipital spine. She suggested that C. prima may represent a sexual variant. The writer agrees that these forms often do occur together, but in the present material no trilobite resembling C. prima has been found. For the time being, it seems best to consider that the broader glabella forms are male and the narrower ones female, since they exhibit bimodal discrepancies such as are commonly correlated with sexual dimorphism (see p. 23). The sexual ratio of the present species is 115.5.

The material comes from a very fossiliferous, light-brown, medium-crystalline limestone, containing C. cordilleare more abundantly than Apomodocia conica, n. gen. et. sp.; the inarticulate brachiopod, Dicellonmus sp., is also common.

Horizon and Locality. Upper Cambrian, Cedaria zone. Princeton, Wasatch Mts., Utah.

Figures specimens. Cranidia ("female"), U.C.M. 38731n, o, q, r, t.
Cranidia ("male"), U.C.M. 38731, p, s, u.

Librigena, U.C.M. 38731w.

Hypostoma, U.C.M. 38731v.

Pygidia, U.C.M. 38731z, a', b'.

Cedarina cordillerae (Howell and Duncan), ontogeny

Anaprotaspid stage (Pl. 7, fig. 1 and text-fig. 42A). The shield is spherical in outline and about 0.26 mm. in length (sag.). A pair of anterior pits, which suggest the orientation of the specimens, are located on the anterior-lateral margin of the shield. The axial and pleural lobes are not differentiated. The surface is nearly featureless except for the covering of fine granules.

Metaprotaspid stage (Pl. 7, figs. 2-4 and text-fig. 42B). The shield is subspherical, convex and about 0.40-0.50 mm. long (sag.). The axial lobe is cylindrical but slightly expanding anteriorly. The anterior pits are rounded, distinct, and seated on the anterior lateral margin of the frontal lobe. The axial rings are not defined, but the terminal tubercle has appeared; it is small, rounded to subrounded, and located at the posterior margin of the shield. A pair of marginal spines project posterior-laterally from the rear margin of the shield. The surface is finely granulose.

This stage is distinguished from the anaprotaspid stage in having the axial and pleural lobes distinctly divided and by the subspherical shield.

Paraprotaspid stage (Pl. 7, figs. 5-8 and text-fig. 42C-E). The subspherical shield consists of a cephalon and protopygidium, and ranges from 0.48 to 0.60 mm. in length. The axial lobe is clearly

defined by dorsal furrows; no axial ring or ring furrows are seen, except for the occipital ring and the protopygidium. The axial lobe is cylindircal but slightly expanding at the mid-length and narrowing slightly both anterior and posteriorly. The pleural lobes are the same width as the glabella or slightly wider. The posterior lateral borders are directly backwardly and terminate in sharply pointed spines. The occipital ring is distinctly marked, transverse, oval, and convex. The protopygidium is transversely subtriangular and curves ventrally behind the posterior margin of the cephalon; the conical and posteriorly tapering axial lobe is divided into one or two axial rings; the pleural lobes are gently convex with two pairs of faint pleural furrows. No marginal spines are preserved. The surface is covered with fine granules.

In this stage the shield is characterized by a distinctly separate cephalon and protopygidium; the posterior lateral fixigenal borders are clearly defined.

Early meraspid stage (Pl. 7, figs. 9-10, 26 and text-fig. 42F). The cranidium is trapezoidal in outline, moderately convex, and varies from 0.55-0.70 mm. in length (sag.). The glabella is slenderly conical, tapering forward, without any distinct glabellar furrows. The occipital ring is definitely separated by an occipital furrow; the occipital spine is directed posteriorly. The anterior border is narrow and is adjacent to the anterior margin of the glabella; no preglabellar field is present. The anterior furrow arches forward and is distinct. The flat to gently convex fixigenae are of the same width as the glabella; their palpebral lobes are medium-size and occur in front of the mid-line

of the glabella (tr.); the posterior lateral fixigenae are transverse and broad; the posterior-lateral borders are narrow; the prominent palpebral ridges arch anteriorly and obliquely to the anterior lateral margin of the glabella. The facial sutures are convergently convex anteriorly and divergently transverse laterally. The pygidium consists of 6 or 7 segments; the posteriorly tapering axial lobe is conical, and 6 or 7 well divided axial rings and ring-furrows; the pleural lobes are about the same width as the axial lobe; the pleural furrow is wide and deep; the interpleural grooves are narrow and distinct; the pleural bands terminate in a pair of short, broad, and posteriorly directed spines. The pygidium may consist of three segments.

This stage differs from the protaspid stage in that the cranidium is trapezoidal in outline, the glabella is slightly conical, the anterior border appears, and the pygidium develops a few thoracic segments.

Late meraspid stage (Pl. 7, figs. 11-13, 25, and text-fig. 42A). The cranidium is triangular in outline, moderately convex, and ranges from 0.80-1.40 mm. long (sag.). The slender, forwardly tapering glabella has three pairs of distinct glabellar furrows; the dorsal furrow is narrow and distinct; the occipital ring is convex with a medium spine directed posteriorly. The anterior brim is divided by a well defined anterior furrow into a narrow preglabellar field and anterior border. The fixigenae are narrower than the glabella and bear palpebral lobes located in front of the mid-line of the glabella (tr.). The pygidium is semi-circular in outline and consists of 3 or 4 segments; there are no marginal spines. The surface is finely granulose.

The definitive features of this stage are as follow: The cranidium appears with a narrow preglabellar field; the fixigenae are narrower than the glabella; the glabella is proportionally shorter and broader; and the pygidium lacks marginal spines. The meraspid stage differs from the holaspid stage in that the meraspid cranidium has a slender glabella; the palpebral lobes are located anteriorly; the fixigenae are wider, and the preglabellar field is narrow. The pygidium of the holaspis is transverse whereas that of the late merapid stage is semi-circular.

Figured specimens. Anaprotaspis, U.C.M. 38731a.

Metaportaspides, U.C.M. 38731b-d.

Paraprotaspides, U.C.M. 38731e-h.

Early meraspides, U.C.M. 38731i, j. y.

Late meraspides, U.C.M. 38731k-m, x.

Family Crepicephalidae Kobayashi, 1935

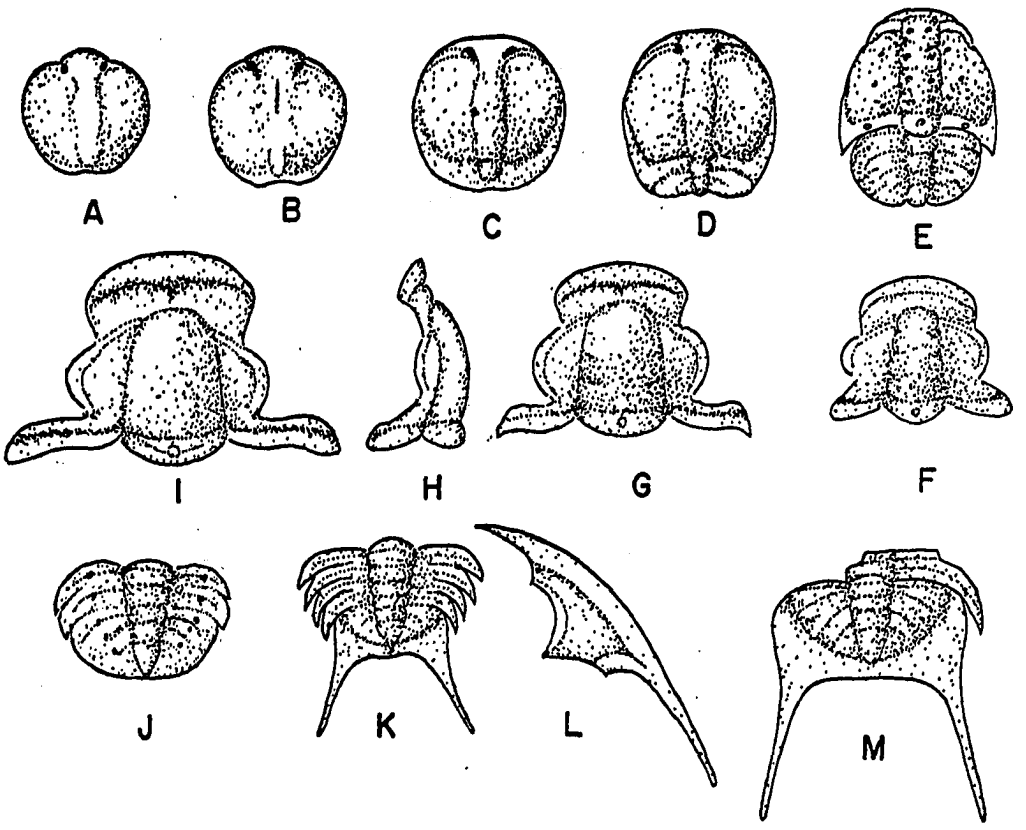
Genus Crepichephalus Owen, 1853

Crepichephalus deadwoodiensis, n. sp.

Pl. 8, figs. 1-29 and text-fig. 43.

Diagnosis. Cranidium trapezoidal in outline, gently convex. Glabella regularly conical with three apirs of short shallow galbellar furrows. Eyes medium-sized and located at the mid-line of the glabella (tr.). Fixigenae and preglabellar field medium narrow. Anterior border generally the same width as preglabellar field and convex. Elongate librigenae moderately convex, with large genal spines. Pygidium subquadrate, transverse, gently convex with 4 or 5 axial rings. Pleural lobes slightly wider than axis. Indistinct marginal border with a pair of posterior lateral spines.

Description. The moderately convex cranidium is trapezoidal in outline. The glabella is conical with a rounded frontal margin. The glabellar furrows are wide and shallowly impressed, all project posterior-medially from the dorsal furrows. The occipital ring is a posterirorly curved crescent bearing a minute tubercle; the occipital furrow is well marked, broad at the center and narrowing toward the sides. The dorsal furrow is deep and wide at the sides of the posterior half of the glabella and shallow across the anterior margin. The fixigenae are moderately narrow, about one-third as wide as the glabella and gently convex at the palpebral lobe area; the posterior lateral lobes are narrow with distinct posterior-lateral furrows and moderately narrow marginal borders. The gently convex preglabellar field is about one-thrid as long as the glabella and slopes downward



Text-fig. 43: Crepicephalus deadwoodiensis, n. sp. A,B, two anaprotaspides, x 65, x 68; C, metaprotaspis, x 63; D, paraprotaspis, x 40; E, an early meraspis, x 21; F,G, two late meraspides, x 16, x 12; H,I, top and side views of an holaspid cranidium, x 5.6; J,K,M, a growth sequence of pygidia, x 27, x 16, x 12; L, librigena, x 17. (Drawings made from photographs.)

toward the broad, shallow anterior furrow; the convex and forwardly arching anterior border is the same width as the preglabellar field; the narrow palpebral lobes are located at the mid-line of the glabella (tr.); they are strongly arched laterally and separated by distinct palpebral furrows. The facial sutures are opisthoparian in form; the anterior branches are convergently convex and the posterior ones are divergently sinuous, almost parallel to the posterior borders.

The elongate librigenae bear medium-sized genal spines; the ocular platform is moderately convex and gently down-sloping towards the lateral border, which is broad and shallowly concave, extending posteriorly to meet the posterior furrow at the genal angle, then continuing onto the genal spine for a short distance; the convex lateral border is generally narrow, but widens slightly posteriorly.

The pygidium is rectangular, transversely broad, and convex; its axial lobe is slightly narrower than the pleural lobes and consists of 4 or 5 axial rings and a smaller terminal portion; the axial furrows are well defined, deeply marked laterally but shallow across the axis. The dorsal furrow is deeply impressed. The pleural lobes slope gently down from the axial lobe, and become flat towards the marginal border; there are three pairs of distinctly impressed pleural furrows, which are shallow and broad; all project posterior-laterally from the dorsal furrows. The marginal border is broad and flat, with an indistinct inner border furrow. A pair of caudal spines with broad bases and slender posterior taper project from the posterior-lateral border. The under side of the pygidium bears a broad and wrinkled doublure.

The skeletal surface is covered with fine granules; the preglabellar field is marked with ridges; and the lateral and anterior borders are ridged. The pygidial margin is finely impressed with wrinkles along the flattened border.

Remarks. This species is represented by 15 adult cranidia and more than 80 immature specimens; all specimens were prepared from a few pieces of light-grey, calcareous interformational conglomerate. The largest cranidium is about 10 mm. long and the smallest immature forms are about 0.25 mm. long (sag.). The prepared specimens exhibit a continuous growth sequence. Both mature and immature forms are present within the intraformational conglomerate clasts and the matrix, indicating that the conglomerate and the matrix formed contemporaneously.

This species is quite similar to C. battsi montanensis Lochman, but differs in having a more rounded glabella, posteriorly located palpebral lobes, and shorter genal spines. It differs from the type species C. iowensis Owen, by possessing a wider anterior border, narrower posterior-lateral fixigenae, and shorter genal spines.

Horizon and Locality. Upper Cambrian, Crepicephalus zone, Deadwood Formation. Lead, northern Black Hills, South Dakota.

Figured specimens. Holotype, Cranidium, U.C.M. 38732.
Paratype, Cranidia, U.C.M. 38732z.
Librigena, U.C.M. 38732y.
Pygidia, U.C.M. 38732, u, w, x.

Cripicephalus deadwoodiensis, n. sp., ontogeny

Anaprotaspid stage (Pl. 8, figs. 1, 2 and text-fig. 43A, B). The

spherical shield varies from 0.23 to 0.25 mm. in length (sag.) and bears a pair of distinct anterior pits and short, broad posterior marginal spines, which suggest the orientation of the shield; the axial and the pleural lobes are not differentiated.

The smallest shield shows no features on the dorsal surface but the larger ones are marked with a longitudinal furrow along the axial region from behind the frontal lobe to the mid-line of the shield (tr.). A tiny elongate node occupies the extreme posterior end of the axial area.

The surface is finely granulose.

Metaportaspid stage (Pl. 8, figs. 3-7 and text-fig. 43C). The spherical to subspherical shield varies from 0.30-0.40 mm. long (sag.). The axial and the pleural lobes are distinctly divided by axial furrows; the axial lobe is fusiform, tapering both forward and backward from the mid-line of the axis (tr.), the axial rings are not well defined; the frontal lobe is delimited by a pair of distinct anterior pits; a pair of short broad supecilioid ridges extend from the posterior lateral margin of the frontal lobe. The occipital ring is delimited by a furrow. The convex pleural lobe is about one and one-half times wider than the axial lobe. A narrow flat fringe surrounds the posterior shield margin. The surface is finely granulose.

Paraprotaspid stage (Pl. 8, figs. 8-10 and text-fig. 43D). The shield is subspherical, about 0.45 to 0.80 mm. in length (sag.), with well differentiated cephalon and protopygidium. The crandium is subrounded to subtriangular in outline, with distinct axial and pleural lobes; the anterior pits are shallow and disappear in the larger

specimens; the frontal lobe tapers from the first segment of the glabella. The occipital ring is convex and transverse. A narrow inward-curing border appears along the anterior margin of the cranidium. The fixigenae are about one and one-half times wider than the glabella and bear a narrow and convex posterior lateral marginal border. The palpebral ridges are prominent; the palpebral lobes are located at one-fourth the length of the glabella (sag.) from the anterior end of the glabella. The facial sutures are present along the anterior-lateral margin and form a convergently convex outline. The protopygidium is transverse; two segments are recognizable. Three pairs of prominent nodes are marked longitudinally on the pleural lobes. The surface of the skeleton is covered with fine granules.

The distinct features of this stage are that the shield is differentitated into cephalon and protopygidium; the facial sutures are present on the dorsal surface; the anterior border is present along the anterior margin, and the fixigenae bear three pairs of large nodes.

Early meraspid stage (Pl. 8, figs. 11-13, 21 and text-fig. 43E). The cranidium is subtrapezoidal in outline and ranges from 1.00 to 1.40 mm. in length (sag.). The glabella is cylindrical and gently rounded anteriorly; it lacks distinct glabellar furrows but bears three pairs of large glabellar nodes. The dorsal furrow is distinct. The occipital ring has a tiny median tubercle. The anterior border curves forward. The fixigenae are the same width as the glabella; the posterior-lateral fixigenae are broadly triangular, with borders projecting posterior laterally. The pygidium of 3 or 4 segments is semi-circular in outline and is associated with three thoracic segments; the axial

lobe is divided into 3 or 4 distinct rings by distinct ring furrows; the pleural lobes are convex and moderately sloping to the margin; three pairs of faintly marked pleural furrows are seen; the posterior marginal border is slightly recessed and flat.

The important characteristics of this stage are that the anterior border curves forward; the glabella becomes cylindrical; the fixigenae are narrower than those of the previous stage; the facial sutures extend directly to the glabella, and pygidium increases in number of segments.

Late meraspid stage (Pl. 8, figs. 14-17, 22, 23 and text-fig. 43F, G). The crandium is subtriangular in outline and about 0.90 to 1.50 mm. in length (sag.). The glabella is slightly cylindrical or conical, without distinct glabellar furrows. The occipital ring is crescentic, with a median tubercle. The dorsal furrow is distinctly marked. The anterior border is convex and about the same width as the preglabellar field; the anterior furrow is distinct and includes a median notch. The fixigenae are about one-half as wide as the glabella. The surface is finely granulose. The rectangular pygidium is preceded by 3 or 4 articulated thoracic segments, and has a pair of short caudal spines projecting posterior-laterally from the rear lateral margin; the axial lobe, which is conical, and tapering posteriorly, is divided into three rings by ring furrows; the pleural bands extend onto the broad and flat marginal border.

This stage differs from the previous one in that the glabella becomes conical; the fixigenae are narrower; the anterior border is wider; and the large pleural nodes have disappeared. The small pygidium

is preceded by 3-4 articulatory thoracic segments and has a pair of short pygidial spines. The meraspis differs from the holaspis in having a slightly cylindrical glabella and wider fixigenae; the pygidium is larger and has a pair of longer pygidial spines.

Figured specimens. Anaprotaspides, U.C.M. 38732a-b.

Metaprotaspides, U.C.M. 38732c-g.

Paraprotaspides, U.C.M. 38732h, j.

Early meraspides, U.C.M. 38732k-m, r.

Late meraspides, U.C.M. 38732n-q, s, t.

Family Alokistocaridae Resser, 1939

Genus Dunderbergia Walcott, 1924

Dunderbergia ? anyta (Hall and Whitfield)

Pl. 9, figs. 1-40 and text-fig. 44.

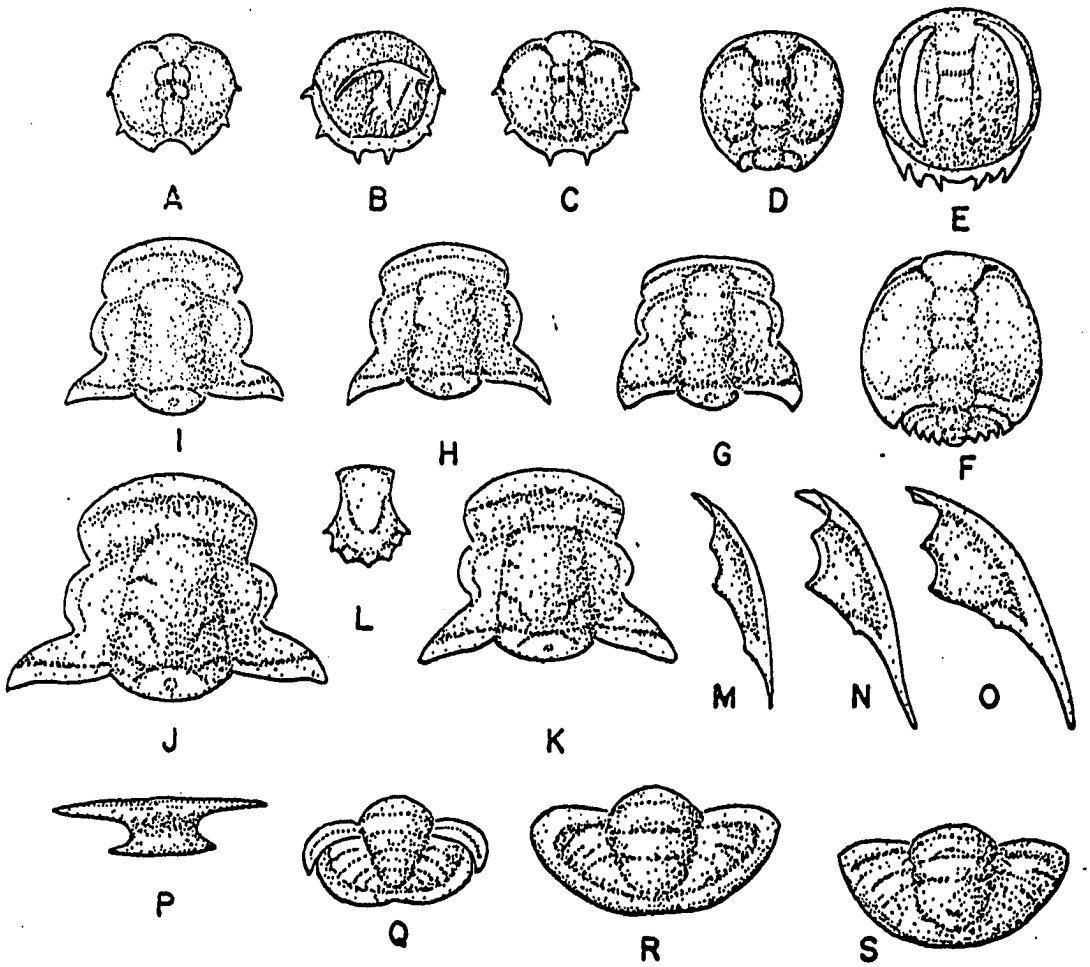
Dunderbergia anytus (Hall and Whitfield), Resser, C. E., 1937, p. 9.

Dunderbergia ? anyta (Hall and Whitfield), Palmer, A. R., 1965, p. 39, pl. 4, figs. 8, 10, 14-16.

Diagnosis. Cranidium trapezoidal in outline. Glabella truncate-conical with rounded anterior margin. Three pairs of faint glabellar furrows. Preglabellar field of medium width. Anterior border convex, about one-half as wide as preglabellar field. Fixigenae narrow, triangular. Hypostoma subquadrate with a medium-sized median body. Librigenae with wide ocular platform and medium-sized genal spine. Rostral plate transverse, with x-shaped outline. Thoracic segments of two different forms: short and long pleural spines. Convex, semi-circular pygidium with axial and pleural lobes of the same width, and consisting of 2 or 3 segments.

Surface covered with fine granules; radial ridges marked on preglabellar field and ocular platform.

The taxonomic analysis of this species was given by Palmer (1965, p. 40) in detail and need not be repeated here. The present material can be segregated into two groups based on the convexity of the skeleton, width and length of glabella, and width of the pygidial margin.



Text-fig. 44: A growth sequence of Dunderbergia ? anyta (Hall and Whitfield). A, anaprotaspis, x 58; B,C, dorsal and ventral views of a metaprotaspis, x 50; D,E,F, paraprotaspides, x 48, x 42, x 40; G, an early meraspis, x 20; H,I, two late meraspides, x 14, x 12; J, "female" cranidium, x 4; K, "male" cranidium, x 7; L, an immature hypostoma, x 46; M-O, a growth series of librigenae, x 16, x 8, x 3.5; P, rostrum, x 8; Q, an immature pygidium, x 26; R, "female" pygidium, x 18; S, "male" pygidium, x 16. (Drawings made from photographs.)

Dunderbergia ? anyta (Hall and Whitfield), male?

Pl. 9, figs. 18,22,24,38,40, and text-fig. 44K, S.

Description. The convex cranidium is trapezoidal in outline. The glabella is truncate-conical with a slightly rounded anterior margin and three pairs of faint, broad glabellar furrows. The dorsal furrow is deeply marked; a pair of pits is impressed on the anterior lateral convexity of the glabella. The narrow occipital furrow is distinct, composide, and branching laterally; the occipital ring is broadly convex and bears a tiny median node. The preglabellar field is one-third as long as the glabella (sag.). The anterior furrow arches forward; it is distinct and steep-sided laterally but becomes shallow across the axis. The convex anterior border is about one-half as wide as the preglabellar field. The fixigenae are flat to gently conves, and less than one-third as wide as the glabella. The palpebral lobes are sickle-shaped, distinctly divided by palpebral furrows, and located in front of the mid-line of the glabella (tr.). The palpebral ridges are faint, obliquely extended to the dorsal furrow, and terminate immediately behind the anterior lateral corners of the glabella. The posterior fixigenae are broad and triangular, with shallow posterior lateral furrows. The posterior lateral borders are convex, wider than the occipital ring and project slightly posterior-laterally. The andterior facial suture-lines are divergently straight to convergently convex at the anterior-lateral border. The posterior ones are divergently sinuate.

The librigenae bear long, slender genal spines. The lateral and posterior furrows are not clearly joined at the genal angle. The

anterior tip of the doublure is blunt, which suggest that the rostral plate has deep, semi-parabolic lateral notch (fig. 23). The platform is convex, and moderately broad.

The moderately convex pygidium is semi-circular in outline. Its axial lobe is broadly conical and tapers slightly backward, divided into two axial rings and a broad terminal portion. The flat to moderately convex pleural lobes are wider than the axis (tr.), and have three pairs of shallow, broad pleural furrows. The marginal furrow is narrow and concave, delimiting a narrow and slightly convex marginal border.

The skeletal surface is covered by fine granules; radial ridges are marked on the preglabellar field and the ocular platform of the librigenae, and fine wrinkles surround the marginal border of the pygidium.

Deunderbergia ? anyta (Hall and Whitfield), female?

Pl. 9, figs. 19-21,25,35,39, and text-fig. 44J, R.

Comparison. In the presumed female form the glabella is narrower and longer than that of the male; the librigenae have narrower platforms and less strongly arched lateral borders; the pygidium is less convex, with a slightly wider marginal border and a median notch on the posterior margin.

Remarks. This species is represented by a few hundred immature and mature specimens, all of which were etched from a single piece of dark-grey, miedium-crystalline limestone. The material also contains Dytrmacephalus granulosus and a few inarticulate brachiopods. The

smallest immature specimen is about 0.25 mm. long (sag.) and has four distinct axial rings and a longitudinal fissure marked along the central axis. These are the significant structures which are also seen in some of the other species described in this report. The larger cranidia, librigenae, and pygidia are morphologically divided into two groups, which have judged sexual dimorphism. The sexual ratio varies 115.

Horizon and Locality. Upper Cambrian, Dunderbergia zone, Wah Wah Range, Utah (U.S.G.S. Coll. No. 5503-CO).

Figures specimens. "Male" form.

Cranidia, U.C.M. 38733o, t.

Librigena, U.C.M. 38733 v.

Pygidia, U.C.M. 38733j, l'.

Rostrum, U.C.M. 38733u.

"Female" form.

Cranidia, U.C.M. 38733p, 38733, 38733r.

Librigena, U.C.M. 38733w.

Pygidia, U.C.M. 38733h', k'.

Hypostoma, U.C.M. 38733b'.

Dunderbergia ? anyta (Hall and Whitfield), ontogeny

Anaprotaspid stage (Pl. 9, fig. 1 and text-fig. 44A). The shield is spherical, about 0.25 mm. in length (sag.), and has three pairs of marginal spines. The axial lobe is fusiform, both ends taper anteriorly and posteriorly from the second pair of axial nodes. The small frontal lobe is delimited by a apir of distinct anterior pits. The second and third axial rings are formed by two pairs of central axial nodes. The

fourth axial ring is subtriangular, and its posterior end is located at posterior margin of the shield. A narrow longitudinal fissure is marked along the central axis. The dorsal furrows are faint. The pleural lobes are about as wide as the axial lobe. The first pair of marginal spines are located at one-third of the total length from the anterior margin; they extend horizontally and laterally. The second pair of marginal spines are short and project posteriorly and laterally from a point two-thrids of the cephalic length posteriorly from the anterior margin. The third pair of marginal spines is short and strong, and project posteriorly from the posterior lateral bases of the terminal axial ring. The surface is covered by fine granules.

Metaprotaspid stage (Pl. 9, figs. 2-6 and text-fig. 44B, C). The convex shield is rounded, about 0.27 to 0.35 mm. in length (sag.), and bears three pairs of marginal spines. The axial and pleural lobes are sharply divided by dorsal furrows. The axial lobe is slenderly fusiform but with a rather expanded frontal lobe. The large frontal lobe is delimited by a pair of anterior pits and dorsal furrows. The second, third, and fourth axial rings are formed by three pairs of axial nodes. The terminal ring is smallest. A longitudinal fissure is marked along the axis. The pleural lobes are about twice as wide as the glabella and are convex with a slightly flat marginal border. The first pair of marginal spines is located in front of the mid-line of the shield (tr.); they are short, with broad bases and project laterally or posterior-laterally. The second pair of marginal spines is shorter than the first; they extend posterior-lateral from points two-thirds of the cephalic length posteriorly from the anterior margin.

The third spines project posteriorly from the posterior margin of the pleural lobes; they are short with broad bases. The narrow posterior marginal border is medially notched.

The underside of the shield shows a narrow rostral plate with a spiny hypostoma anteriorly and broad doublure posteriorly. The narrow rostral plate is perrostral in form, and its posterior projections in front of the third pair of marginal spines, where the doublure appears. The hypostoma is broadly fusiform with a fused rostral plate anteriorly and spiny margin posteriorly; the triangular median body is narrow with distinct lateral furrows; the first pair of marginal spines is broad, short; they extend laterally from the mid-length of the hypostoma (tr.). The second and third pairs are short, and project posteriorly and laterally along the posterior lateral margin. The terminal spine is longer and extends posteriorly from the axial line. The doublure is broad and rounded along the posterior margin of the shield from the first pair of marginal spines.

The surface of the shield is finely granulose.

The characters of this stage which are different from those of the early ones are the presence of five rings on the axial lobe, and the larger frontal lobe.

Paraprotaspid stage (Pl. 9, figs. 7-12 and text-fig. 44D-F). The shield is sepherical in outline and ranges from 0.40-0.60 mm. long (sag.). The cylindrical glabella is composed of four distinctly separated rings; the first ring, or frontal lobe, is large and expanded anteriorly; the second to fourth ones are transverse, oval, and uniform. The occipital ring is convex, oval, and separated by occipital furrows.

The elongate anterior pits are shallowly impressed in the dorsal furrows and delimited by a pair of short, laterally projecting eye-brow-shaped ridges from the anterior lateral margin of the frontal lobe. The pleural lobe are approximately one and one-half times as wide as the glabella; the posterior borders are well-defined and project posterior-laterally. The protopygidium is subtriangular, with one or two axial rings and sharp, laterally directed pleural spines. The underside of the shield shows a narrow doublure along the protopygidial margin. The hypostoma has reduced marginal spines and a widened median body. The surface is covered by fine granules.

This stage is characterized by the appearance of the protopygidium,, the fusion of the axial nodes, and the separation of the rostral plate, librigenae, and hypostoma.

Early meraspid stage (Pl. 9, figs. 13,14,27,28,33, and text-fig. 44G.). The cranidium is trapezoidal in outline and varies from 0.70-1.00 mm. in length (sag.). The glabella is cylindrical or slightly constricted at the second glabellar ring. The glabellar rings are all nearly of the same form and separated by shallow glabellar furrows. The glabellar furrows are shallow across the central axis and steep-sided. The dorsal furrows are distinct. The convex occipital ring is crescentic and arches posteriorly. The narrow anterior border appears; it is convex and curves anteriorly. The palpebral lobes are narrow, distinctly divided by palpebral furrows, and located in front of the mid-line of the glabella (tr.). The fixigenae are of about the same width as the glabella. The posterior fixigenae are broad; the posterior borders with their lateral ends directed posterior-laterally. The elongate libri-

genae each have a narrow ocular platform and a medium-sized genal spine. The hypostoma is about 1.2 mm. in length, with an elongate, oval median body; the lateral furrows are deep and narrow. The posterior lobe is U-shaped and broadly convex; the marginal border is narrow and separated by distinct marginal furrows; the first lateral marginal spines are larger and stouter than the following ones, which occur at the lateral margins of the mid-line of the hypostoma (tr.); the posterior marginal spines are small and are located along the posterior marginal border. The pygidium is approximately 1.2 mm. in length and bears 5 or 6 marginal spines; the axial lobe is divided into 5 or 6 axial rings; the pleural lobes are separated into pleural bands by distinct interpleural grooves; the marginal spines extend continuously from the pleural bands; they are turned upward and project posterior-laterally. The pygidium may connect to a few articulated thoracic segments. The surface of the skeleton is covered by moderately large granules.

The definitive characteristics of this stage are: the cranidium has a narrow anterior border; the glabella is cylindrical; the dixigenae are the same width as the glabella; the librigenae are narrower and the pygidial segments are preceded by a few thoracic segments.

Late meraspid stage (Pl. 9, figs. 15-17,26,29,34,35,37 and text-fig. 44H, I). The cranidium is trapezoidal in outline, about 1.20-1.80 mm. in length (sag.). The glabella is conical and marked by three pairs of distinct glabellar furrows. The dorsal furrows are narrow and distinct. The preglabellar field is about the same width as the anterior border. The fixigenae are narrower than the glabella. Each libri-

genae has a narrow ocular platform. The pygidium bears a conical axial lobe, which is divided by ring furrows; a median notch at the posterior margin. The surface is finely granulose, and radial ridges are marked on the preglabellar field.

The specimens of this stage are distinguished from those of early forms in that the crandium has a conical glabella, the preglabellar field appears, the fixigenae are narrower than the glabella, and each librigena has a broad ocular platform; the pygidium shows the general outline seen in the holospid pygidium, except that a median notch is marked at the posterior margin, and the pygidium is preceded by one or two thoracic segments.

Figured specimens. Anaprotaspis, U.C.M. 38733a.
Metaprotaspides, U.C.M. 38733b-e.
Paraprotaspides, U.C.M. 38733f-j.
Early meraspides, U.C.M. 38733k, l, y, z, e'.
Late meraspides, U.C.M. 38733m, n, o, x, a', f', g', i'.

Family Pterocephaliidae Kobayashi, 1935

Genus Dytremachephalus Palmer, 1954

Dytremacephalus granulosus Palmer

Pl. 10, figs. 1-36 and text-fig. 45

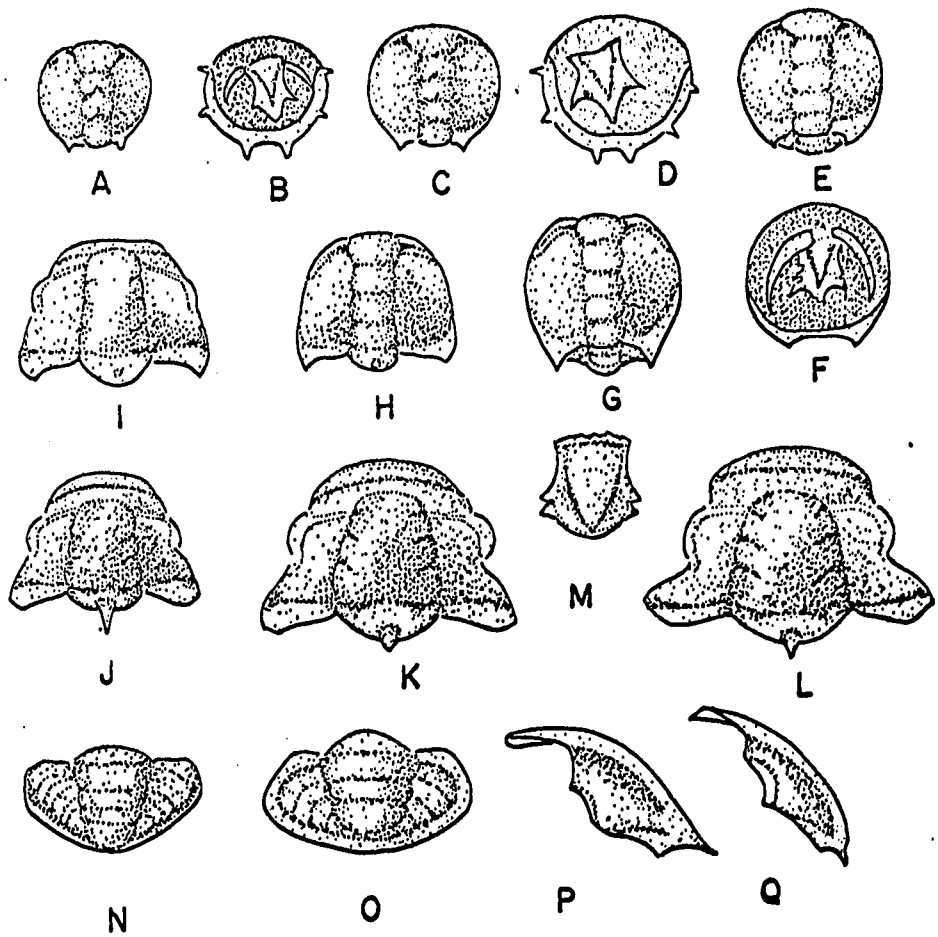
Dytremacephalus granulosus Palmer, A. R., 1954, p. 750, pl. 85, figs. 5 and 6; and 1965, p. 85, pl. 18, figs. 14, 16-19, 21.

Diagnosis. Cranidium trapezoidal in outline. Glabella broadly conical with three pairs of glabellar furrows. Occipital ring bearing a short median spine. Preglabellar field moderately narrow. Anterior border about the same width as preglabellar field. Fixigenae about one-thrid as wide as glabella. Palpebral lobe situated in front of the mid-line of glabella (tr.). Anterior facial suture lines convergently convex, and posterior facial suture lines divergently straight. Each librigena with broad ocular platform and short genal spines. Pygidium highly convex, semi-circular in outline, having broadly conical axial lobe. Surface covered by moderately large granules.

Dytremacephalus granulosus Palmer, male?

Pl. 10, figs. 21,23,25,26,28,35, and text-fig. 45L, N.

Description. The cranidium is trapezoidal in outline. The glabella is broadly conical, with three pairs of well defined glabellar furrows. The occipital furrow curves slightly backward and is deeply impressed laterally. The occipital ring is crescentic and has a short prominent median tubercle. The preglabellar field is steeply declined and strongly depressed laterally. The anterior furrow is shallow and



Text-fig. 45: Dytremacephalus granulosus Palmer. A, anaprotaspis, x 56; B,C, ventral and dorsal views of two metaprotaspides, x 55; D, ventral view of a metaprotaspis, x 58; E,F,G, ventral and dorsal views of two paraprotaspides, x 62, x 50; H, a late paraprotaspis, x 42; I, an early meraspis, x 25; J, a late meraspis, x 15, K, a "female" cranidium, x 9; L, a "male" cranidium, x 10; M, an immature hypostoma, x 15; N, a "male" pygidium, x 13; O, a "female" pygidium, x 15; P,Q, juvenile and adult librigenae, x 9, x 22. (Drawings made from photographs.)

broad. The anterior border is arched forward, convex, and about the same width as the preglabellar field. The flat to slightly convex fixigenae are approximately one-third as wide as the glabella. The palpebral lobes are well-defined by palpebral furrows, located in front of the mid-length of the glabella (tr.). The posterior lateral fixigenae are convex and triangular. The posterior borders are more than one-half as wide as the occipital ring(tr.). The posterior fixigenal furrows are deeply impressed laterally. The anterior branches of the facial sutures are convergently straight, and posterior branches are gently divergent.

Each librigena has a broad ocular platform. The lateral furrow is shallow, wider and becomes obsolete posteriorly before meeting the rear border furrow. The lateral border is roundly convex and has a long and sharply pointed anterior projection. The doublure is the same width as the lateral border. The posterior border furrow is deep but shallow towards the genal angle. The genal spine is short and sharply pointed posterior-laterally.

The thoracic segments are highly convex; their axial rings are slightly narrower than the pleural lobes and deeply separated by ring furrows. The anterior half-ring is crescentic, convex and arching forward. The posterior ring is delinited by a ring furrow and is about the same width as the half-ring. Each pleural lobe is flat laterally for a short distance and slopes steeply downward to form a long and sharply pointed pleural spine.

The pygidium is semi-circular in outline; the dorsal lobe is divided into two axial rings and a large terminal portion. The pleural

lobes are narrower than the axis and moderately convex anterior-laterally, and progressively deflect posteriorly. The flat marginal border is of medium width and delimited by a poorly defined inner marginal furrow; the pleural lobes are shallowly impressed by 2 or 3 pleural furrows; all curve posteriorly and laterally to reach the inner edge of the border.

The surface of the skeleton is covered by moderately large granules; ridges occur along the anterior cephalic margin.

Dytremacephalus granulosus Palmer, female?

Pl. 10, figs. 20,22,27,36, and text-fig. 45K, O.

Comparison. The presumed female specimens differ from those of the males in having a narrower conical glabella with a rounded anterior margin; each librigena has a wider ocular platform, and the triangular pygidium has a narrower marginal border.

Remarks. A few hundred immature and mature specimens were etched from a small piece of dark-grey, medium-crystalline limestone. The material also contains immature and mature forms of Dunderbergia ? anyta and several inarticulate brachiopods. The immature specimens of these two trilobite genera are quite different when compared with the same sized instars of the present species: those of Dytremacephalus granulosus are strongly convex, the glabella is marked with four complete axial rings, the hypostoma has one pair of lateral spines, and the pygidial marginal spines are shorter and broader; whereas, those of Dunderbergia ? anyta have a low convex shield; the axial lobe is occupied by 2 or 3 pairs of axial nodes; the hypostoma has three

pairs of posterior marginal spines; and the pygidial marginal spines are more slender and longer. The sexual ratio is 135.6.

Horizon and Locality. Upper Cambrian, Dunderbergia zone, Wah Wah Range, Utah (U.S.G.S. Coll. No. 5503-Co.).

Figured specimens. "male" form.

Cranidia, U.C.M. 38734s, v.

Pygidium, U.C.M. 38734g'.

Librigena, U.C.M. 38734z.

Thoracic segments, U.C.M. 38734w, x.

"female" form.

Cranidia, U.C.M. 38734r, t.

Pygidium, U.C.M. 38734h'.

Librigena, U.C.M. 38734y.

Dytremacephalus granulosus Palmer, ontogeny

Anaprotaspid stage (Pl. 10, fig. 1, and text-fig. 44A). The highly convex shield is rounded to subrounded in outline, with well marked dorsal furrows. It is about 0.23 to 0.25 mm. long (sag.). The axial lobe is divided into four axial rings by well defined transverse furrows; the frontal lobe is large, convex, and delimited by a pair of anterior pits; the lateral margin of the frontal lobe is continuous with a pair of supercilioid ridges; the second and third rings are transversely subrounded; the terminal one is rounded; a minute ridge extends along the central axis. The pleural lobes are convex and slightly wider than the glabella (tr.). The presumed marginal spines are not preserved. The surface is covered by fine granules.

Metaprotaspid stage (pl. 10, figs. 2-6 and text-fig. 44 B, C). The shield is rounded, rather convex, and approximately 0.26-0.27 mm. long (sag.). It bears three pairs of marginal spines and the surface is well divided into axial and pleural lobes by distinct dorsal furrows. The axial lobe consists of five rings; the frontal lobe is triangular with a pair of eye-brow-shaped ridges projecting laterally and posteriorly from the anterior lateral margin; the second, third, and fourth rings are transversely subrounded and of subequal size; the posterior one is the smallest. The anterior pits are well-defined and elongated along the sides of the frontal line. The convex pleural lobes slope downward toward the rather narrow marginal border. The hypostoma is elongately pentagonal in outline, with a straight anterior margin, and a pair of stout lateral spines projecting posterior-laterally; the median body is elongate-triangular, defined by lateral furrows. The underside of the shield is surrounded by a narrow, rounded doublure along the posterior half of the shield margin. The surface is covered by fine granules; the pleural lobes are marked with a few pairs of minute transverse furrows, which possibly are the vestigial cephalic segmental furrows (fig. 5).

Paraprotaspid stage (Pl. 10, figs. 7-14 and text-fig. 45E-G). The shield is spherical ranging from 0.29 to 0.40 mm. in length (sag.), and having three pairs of marginal spines at the shield margin (fig. 8). The pleural and axial lobes are divided by dorsal furrows; the cylindrical axial lobe is only slightly expanded forward; the large frontal lobe is convex and expanded forward with a pair of narrow supercilioid ridges projecting laterally from the anterior lateral margin.

The second to fourth axial rings are transverse and are all of subequal size; the terminal ring is small. The elongate anterior pits are located along the dorsal furrows at the posterior lateral margin of the frontal lobe. The pleural lobes are convex and about one and one-half times as wide as the glabella. The first pair of marginal spines is located on the anterior-lateral margin of the shield; the second ones are located laterally; the third are situated posteriorly and project from the extreme ends of the posterior lateral border. The protopygidium is transversely subtriangular with one or two segments. The underside of the shield exhibits the perrostral plate and hypostoma anteriorly and the narrow doublure along the posterior margin of the protopygidium. The surface is covered by fine granules.

The specimens of this stage are subspherical with well defined cephalic and pygidial shield; the larger specimens possess only one pair of spines, which are at extreme ends of the posterior lateral border of the cephalon; the transverse pleural furrow and the axial ridge are absent.

Early meraspid stage (Pl. 10, figs. 15-17,24,29-32 and text-fig. 45I). The cranidium is trapezoidal in outline, highly convex, with a well defined anterior border and facial sutures. It varies from 0.50-0.80 mm. in length (sag.). The glabella varies from cylindrical to slightly conical. It is divided into three glabellar segments by complete glabellar furrows; the glabellar furrows are shallow, faint, and directed slightly postero-medially from the dorsal furrows; the occipital ring is broadly convex and crescentic with a tiny median tubercle. The anterior border is narrow, arching forward, and sharply

defined by the anterior furrow. The dorsal furrow is distinct. The convex fixigenae are subequal in width to the glabella. The posterior-lateral fixigenae are broad, well defined by border furrows and borders; the width (tr.) of the posterior border corresponds with the width (tr.) of the occipital ring; the narrow, elongated palpebral lobes are located at the first pair of glabellar furrow in the smaller specimens but move posteriorly to the second glabellar in the larger ones. The facial suture lines are convergently straight anteriorly and divergently straight posteriorly from the palpebral lobes. The convex hypostoma is elongate-pentagonal; its anterior margin is straight or slightly arching forward; the lateral spines are located slightly posteriorly from the mid-length of the median body. They extend laterally and slightly posteriorly. The posterior marginal border is convex posteriorly; the median body is narrowly triangular, convex, wedge-shaped, and sharply pointed posteriorly to the posterior margin; the lateral furrows are distinct, deeply marked at the mid-length, and shallow both anteriorly and posteriorly. Each librigena is narrow with an ocular platform of almost uniform width; the genal spine is very short and broad, projecting psoterior laterally. The pygidium is transversely subspherical with a narrow, convex axial lobe and wider pleural lobes; the axial lobe of 6 or 7 axial rings is conical and tapers sharply posteriorly. The pleural lobes are moderately convex, broad, each having pleural bands running slightly posterior-laterally and ending with a broad terminal spine; the pleural furrow is broad and shallow, and the interpleural grooves are minute. The surface is covered with fine granules. The pygidial axis bears a small tubercle

on each ring.

The specimens of this stage are characterized by a forward-tapering glabella, well separated glabellar segments, distinct anterior border, pygidium preceded by 2 or 3 articulated thoracic segments, and librigenae of uniform width posteriorly and anteriorly.

Late meraspid stage (Pl. 10, figs. 18,19,33,34, and text-fig. 45S). The cranidium is trapezoidal in outline and about 1.0 to 1.5 mm. in length (sag.). The glabella is conical with a rounded frontal margin; the glabellar furrows are impressed, except for the first pair which are faint. The occipital ring is broad, with a tiny median spine extending posteriorly. The fixigenae are about one-half as wide as the glabella but have broad posterior lateral portions. The palpebral lobes are small and located next to the second glabellar furrows (tr.). The palpebral ridges are prominent and project obliquely to the anterior-lateral margin of the glabella. The facial suture lines are convergently straight anteriorly and divergently straight posteriorly. The pygidium is transversely semi-circular and has a median notch at the posterior margin. It is associated with one or two thoracic segments. The surface is covered by distinct granules.

This stage differs from the previous one in having a slender, conical glabella, the palpebral lobes located at the level of the second glabellar furrow, a narrow preglabellar field, the pygidium separated from the cephalon by one or two thoracic segments, and a notch at the posterior margin.

Figured specimens. Anaprotaspis, U.C.M. 38734a.

Metaprotaspides, U.C.M. 38734b-e.

Paraprotaspides, U.C.M. 38734f-l.

Early meraspides, U.C.M. 38734m-o, u, a'-d'.

Late meraspides, U.C.M. 38734p, q, e', f'.

Family Ptychaspididae Raymond, 1924

Genus Ptychaspis Hall, 1863

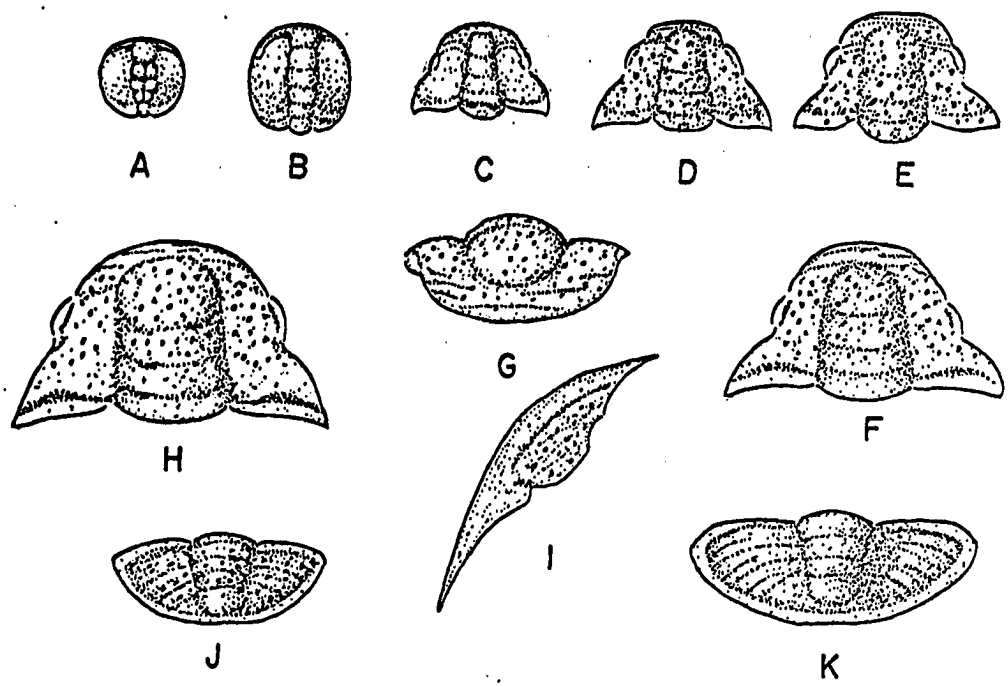
Ptychaspis bullasus Lochman and Hu

Pl. 11, figs. 1-34 and text-fig. 46.

Ptychaspis bullasa Lochman, C. B., and Hu, C. H., 1959, p. 422, pl. 58, figs. 21-42; Bell, W. C., and Ellinwood, H.L., 1962, p. 405, pl. 58, figs. 14-17.

Diagnosis. Convex crandium trapezoidal in outline. Glabella nearly parallel-sided, with rounded frontal margin and two transverse glabellar furrows. Occipital ring crescentic and convex, bearing a median tubercle. Frontal margin narrow and strongly convex. Fixigenae convex, about one-third as wide as glabella. Palpebral lobes located in front of the mid-length of glabella. Posterior fixigenae broadly triangular. Librigenae elongate with a broad-based genal spine. Hypostoma narrow, elongate, with a convex median body and broad triangular wings. Pygidium narrowly transverse, with broad axial lobe and narrow vertically upturned marginal border. Surface densely granulose with large granules, and well elevated ridges are marked along the skeletal margin.

Description. The cranidium is trapezoidal in outline with a rounded anterior border. The dorsal furrows are deeply impressed and broad. The glabella is broadly cylindrical, convex, long, nearly parallel-sided with a rounded anterior margin. The first pair of glabellar furrows is faint; the second and third ones are transverse, deeply impressed laterally but shallow across the central axis. The occipital ring is crescentic with a small median node; the occipital



Text-fig. 46: Ptychaspis bullasus Lochman and Hu. A, metaprotaspis, x 45; B, paraprotaspis, x 35; C,D, two early meraspides, x 20, x 13; E, a late meraspis, x 12; F, G,H, three holaspides, x 8.6, x 3, x 2.7; I, librigena, x 6.6; J,K, a small and a larger sized pygidium, x 8, x 3. (Drawings made from photographs.)

furrow is broad and deep. The frontal area is narrow, convex and steeply declined; the anterior margin is vertical with a blunt median point. The fixigenae are horizontal, slightly convex and more than half as wide as the glabella; the small and narrow palpebral lobes are separated by deeply marked palpebral furrows situated opposite the anterior one-third of the glabella. The posterior fixigenae are broadly triangular, and extend slightly posterior-laterally; the narrow posterior-lateral borders are defined by broad posterior-lateral furrows; the width (tr.) of the rear lateral border is the same as that of the occipital ring (tr.).

Each librigena is elongate with an ocular platform bearing a small ocular ring; the lateral and posterior furrows join at an acute angle, where they are shallow; they are deeper anteriorly and laterally; the convex lateral border is of medium width and gently deflected along the margin; it is continuous posteriorly with a long and broad-based genal spine.

The pygidium is transversely semi-circular in outline and moderately covex; the axial lobe is broad, parallel-sided to slightly tapering backward and divided into three well-marked axial furrows and a broad terminal portion, which has a pair of nodes on the posterior lateral margin. The pleural lobes are board, with three shallow but well defined pleural furrows and the same number of narrow interpleural grooves. The marginal border is narrow and upturned vertically; the posterior marginal border is slightly indented medially.

The surface is covered by large granules, except in the furrows and well elevated, irregular ridges are marked along the skeletal margin.

Remarks. This species is represented by more than 30 adult and 20 immature specimens. The materials are those described in 1959 by Lochmand and Hu. The present work attempts a more detailed analysis of the ontogenetic development of the species. The materials also contain some meraspides of Minkella ("Saratogia") americana (Lochman and Hu) and Idahoia wisconinensis (Owen). The differences between them are obvious. The present species has a more convex shield, a more slenderly conical or nearly fisiformed glabella, and broader fixigenae, whereas those of the other two genera have less convex cranidium, cylindrical glabella, and narrower fixigenae.

Horizon and Locality. St. Charles Formation, Upper Cambrian, Ptychaspis-Prosaukia zone. North of Mink Creek, Preston quadrangle, Idaho.

Figured specimens. Cranidia, U.C.M. 38735, 38735m-s.
Librigenae, U.C.M. 38735t-v.
Pygidia, U.C.M. 38735y, z and
U.S.N.M. 137100h.

Ptychaspis bullasus Lochman and Hu, ontogeny

Metaprotaspid stage (Pl. 11, fig. 1, and text-fig. 46A). The shield is about 0.24 mm. in length with separate axial and pleural lobes. The axial lobe is composed of a big frontal lobe, three pairs of axial nodes, and a samll terminal ring; the frontal lobe is rounded and convex, delimited by a pair of deeply marked anterior pits on its anterior-lateral margins; the three pairs of axial nodes are divided by longitudinal fissure along the axis and transverse furrows across the

axis; a small terminal tubercle is present near the posterior margin of the shield. The pleural lobes are convex and gently down-sloping toward the marginal border. The surface is covered by fine granules.

Paraprotaspid stage (Pl. 11, figs. 2-4 and text-fig. 46B). The shield is spherical to subspherical in outline and about 0.28 to 0.45 mm. in length (sag.). The axial lobe is delimited by dorsal furrows and is cylindrical to slightly fusiform; it is composed of five axial rings and a small protopygidial ring; the glabellar or axial rings are transverse, oval, convex, and connected by a faint median ridge along the central axis; the anterior pits are shallower than in the meta-protaspis but well defined. A very narrow border appears along the anterior margin of the shield. The pleural lobes are the same width as the glabella, and marked by a pair of distinct palpebral lobes at the anterior lateral margin. The posterior-lateral borders extend laterally from the sides of the occipital ring with a pair of posteriorly directed spines at the extreme ends. The protopygidium is narrow, transverse, and curves ventrally from the posterior cephalic margin; one or two segments may be present, but the nature of the pleural lobe is obscure.

This stage is distinguished from the previous one in that the three pairs of axial nodes are fused together to form three axial rings; the anterior border and palpebral ridges are recognizable, and the protopygidium appears.

Early meraspid stage (Pl. 11, figs. 5-7,29,30 and text-fig. 46C, D). The cranidium varies from 0.50-1.00 mm. in length (sag.), is trapezoidal in outline with a rounded anterior border. The axial lobe

tapers slightly forward and is sub-hemicylindrical in configuration; the first axial ring furrow is faint, but the following furrows are deeper, wider, and strongly impressed laterally. The occipital ring is deeply separated by the occipital furrow and bears a median spine. The pleural lobe is narrow and triangular with palpebral lobes located opposite (tr.) the first glabellar furrows; the posterior lateral borders are delimited by border furrows and have posterior-lateral projections. The pygidium consists of 6 or 7 segments with short blunt marginal spines; it may retain a few articulated thoracic segments. The surface is densely covered with large granules.

The distinguishing characteristics of this stage are: the somewhat conical axial lobe with three long axial rings anteriorly and two short ones posteriorly (sag.).

Late meraspid stage (Pl. 11, figs. 8-13,26,27,31, and text-fig. 46E). The trapezoidal cranidium is about 1.1-1.80 mm. in length (sag.). The glabella is conical with a rounded frontal margin. The first pair of glabellar furrows is faint, shallow, and separated. The second and third ones are deeper and extend slightly backward. The occipital furrow is as deep and as wide as the third glabellar furrow; the occipital ring is convex and bears a median tubercle. The narrow fixigenae are divided by palpebral furrows and located opposite (tr.) the second glabellar furrows. The librigena is broad, crescentic, with lateral and posterior furrows, connected at the genal angle; the genal spine is short with a broad base. The pygidium is subtriangular in outline, and has the axial and pleural lobes divided into three segments by furrows; the pleural lobes are broad and deep; the interpleural

grooves are narrow and minute.

The surface is covered by large granules, and irregular ridges are marked along the anterior cephalic margin and ocular platform.

In comparison, the skeleton of this stage differs from those of early ones in that the glabella is wider and shorter; the pygidium is generally of holaspid shape. The meraspid specimens differ from holaspis forms by their conical glabella, palpebral lobes located at the second glabellar furrow (tr.), and librigenae with wider ocular platforms and shorter genal spines. The pygidium lacks a posterior median notch and is semi-circular.

Figured specimens. Metaprotaspis, U.C.M. 38735a.

Paraprotaspides, U.C.M. 38735b-d.

Early meraspides, U.C.M. 38735e-f, w, x.

U.S.N.M. 137100a.

Late meraspides, U.C.M. 38735g-l, q.

Family Olenidae Burmeister, 1843

Genus Olenus Dalman, 1827

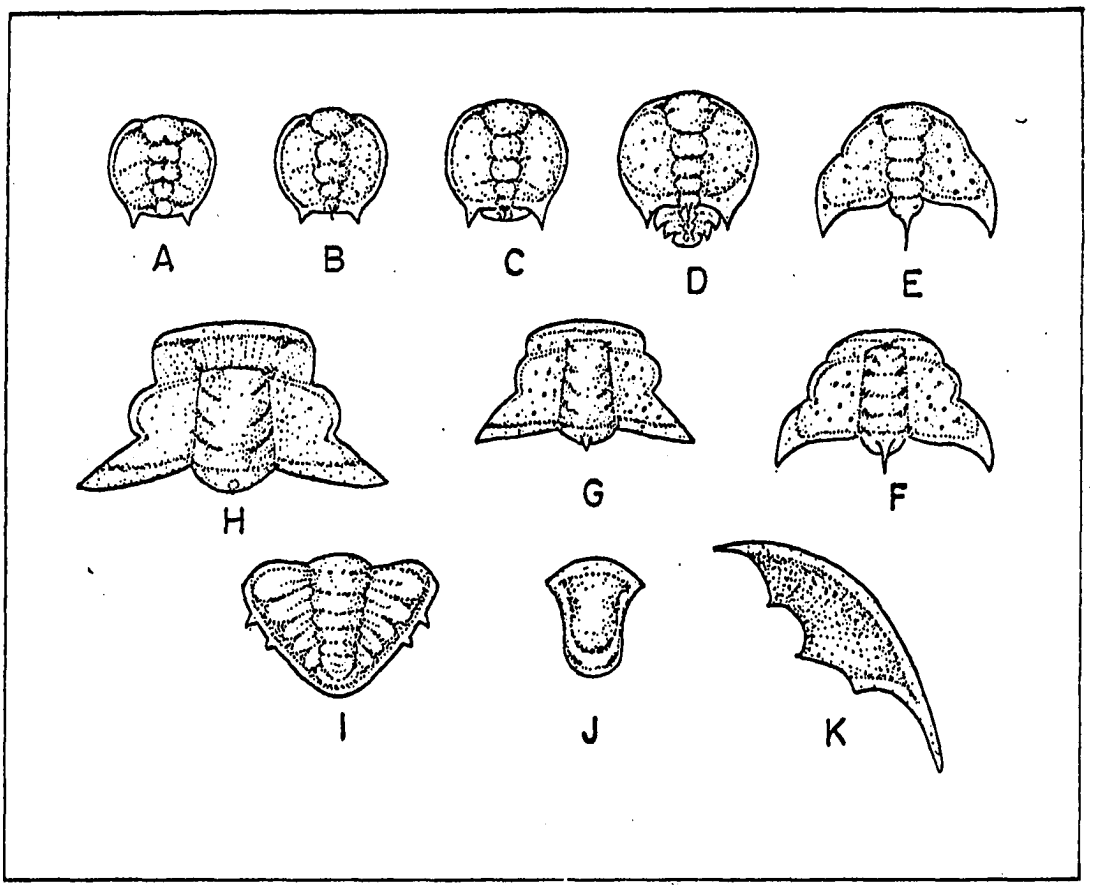
Olenus gibbosus (Wahlenberg)

Pl. 12, figs. 1-32, and text-fig. 47

Entomostracites gibbosus Wahlenberg, G., 1821, p. 39, pl. 1, fig. 4 only. Olenus gibbosus (Wahlenberg), Angelin, N.P., 1878, p. 44, pl. 25, fig. 5; Strand, T., 1927, p. 320-329, pl. 2, fig. 1-14d; Størmer, L., 1942, pl. 81, figs. 9a-e, and 10a-e; Henningsmoen, G., 1957, p. 105, pl. 1, fig. 1, pl. 3, and pl. 9, fig. 7.

Diagnosis. Cranidium trapezoidal in outline, moderately convex with a truncate-concial glabella. Dorsal furrow deeply impressed. Fixigenae broad with the palpebral labe located at the mid-length of crandium. Librigena of medium width; genal spine continuous with course of lateral margin. Pygidium subtriangular with 1 or 2 pairs of marginal spines and 5 or 7 axial rings. Hypostoma subquadrate in outline, with a large convex median body.

Description. The trapezoidal crandium is moderately convex; the glabella is truncate-conical, tapering slightly forward, with three pairs of oblique lateral furrows; the preglabellar field is gently convex, more than one-half the length of the glabella (sag.); the anterior border is narrow and separated by a distinct anterior furrow; the fixigenae are broad and more than one-half the width of the glabella (tr.); the palpebral lobes are moderately small and located slightly in front of the mid-line of the glabella (tr.); the palpebral ridges are at a right angle to the anterior-lateral corners of the glabella; the occipital ring bears a small node. The librigena bears



Text-fig. 47: A growth series of Olenus gibbosus (Wahlenberg). A,B, two metaprotaspides, x 50; C,D, two paraprotaspides, x 50, x 30; E,F, two early meraspides, x 20, x 18; G, a late meraspis, x 10; H, holaspid cranidium, x 7; I, a pygidium, x 7; J, hypostoma, x 20; K. librigena, x 4. (Drawings made from photographs.)

a broad ocular platform and a medium-sized genal spine. The convex and elongate hypostoma is subquadrate in outline and has a large median body. The flat pygidium is triangular in outline and has 5 to 7 axial rings and furrows; the pleural lobe is flat, gently uptruned from the dorsal furrow, with well developed pleural furrows; a pair of marginal spines extend from the anterior-lateral corners of the pygidium.

The surface of the skeleton is covered by fine granules, and minute radial ridges occur on the preglabellar field and the platforms of the librigenae.

Remarks. The ontogeny of this species was first established by Strand (1927) and subsequently re-examined by Størmer (1942). The material here studied was collected by K. E. Caster during a field trip of the International Geologic Congress, 1962. More than 90 immature and mature skeletons have been freed from a small piece of fossiliferous bituminous limestone. The smallest specimen is 0.27 mm. long and the largest cranidium about 15.0 mm. in length.

Størmer's observation that the earliest instars have the cephalic segmental furrows impressed on the pleural lobes is correct, but they are very minute and almost impossible to sbserve. In addition, a few instars were found in which the axial lobe contains five rings, of which two are formed by four axial nodes, situated in between the frontal lobe and posterior two rings (fig. 1-3). These are similar to features occurring in other young trilobites, which are described in this report.

Horizon and Locality. Upper Cambrian, Zone II, Ringsaker Station, north of Oslo, Norway.

Figured specimens. Cranidia, U.C.M. 38736 and 38736s, d', e'.

Hypostoma, U.C.M. 38736t, u.

Librigenae, U.C.M. 38736x, y.

Pygidia, U.C.M. 38736b', c'.

Olenus gibbosus (Wahlenberg), ontogeny

Metaprotaspid stage (Pl. 12, figs. 1-3 and text-fig. 47A, B). The moderately convex shield is spherical to subspherical in outline and about 0.27 mm. in length (sag.). The glabella is composed of a large frontal lobe, two pairs of axial nodes, and two small posterior axial rings. A minute fissure is impressed along the axis of the glabella (sag.). The dorsal furrow is well-developed. The pleural regions are gently convex, with 3 or 4 poorly defined cephalic segmental furrows. The marginal border is limited by an indistinct marginal furrow. The marginal spines are obscure except for the posterior pair. The surface is covered by fine granules.

Paraprotaspid stage (Pl. 12, figs. 4-8 and text-fig. 47C, D). The shield is circular in outline and about 0.30-0.40 mm. in length (sag.). The axis is expanded anteriorly and divided by faint, transverse furrows. The frontal lobe, which consists of a pair of eye-brow-like ridges is larger than most of the axial rings. The anterior pits are shallow and elongate; the pleural lobe is about one and one-half the width of the glabella (tr.), and is surrounded by a narrow marginal border. The prominent palpebral ridge extends from behind the anterior pit and posterior-lateral margin of the frontal lobe and curves laterally and posteriorly to the marginal border. The marginal spines are obscure, except for the posterior pair, which are produced from the

posterior-lateral margin.

The protopygidium appears at the posterior margin of the shield, curving ventrally between the posterior spines. It is triangular and consists of two segments. The surface of the shield is covered by fine granules.

The new features in this stage are: the fusion of the two pairs of metaprotaspid glabellar nodes to form two complete glabellar rings; the pleural segmental furrows are not visible; the protopygidium appears; and a pair of short furrows are newly developed on the sides of the frontal lobe.

Early meraspid stage (Pl. 2, figs. 9-12, 29 and text-fig. 47E, F). The trapezoidal shield is about 0.50-0.85 mm. in length (sag.). The glabella is hemi-cylindrical to slightly expanded anteriorly. The frontal lobe is larger than the following axial ring, and bears a pair of short furrows laterally. The prominent palpebral ridges extend from the lateral margin of the frontal lobe and are located slightly posterior to their position in the earlier stage. The anterior pits are absent. The posterior lateral border is expanded laterally with a pair of posterior spines at the extreme ends. The pygidium is elongated, sub-triangular, with five distinct axial rings. The pleural lobes are slightly convex above the dorsal furrow; the narrow marginal border bears short marginal spines, which are continuous projections of the pleural segments. The surface is covered by medium sized granules.

The important features of this stage are: the trapezoidal outline of the crandium, the hemi-cylindrical form of the glabella, and the first appearance of the anterior border.

Late meraspid stage (Pl. 12, figs. 13-18,25,26,30 and text-fig. 47G). The trapezoidal crandium is about 0.90 to 1.50 mm. in length (sag.) and moderately convex. The conical glabella is marked by three pairs of glabellar furrows, which are deeper laterally and become more shallow toward the axis. The occipital ring is convex and bears a tiny median tubercle. The dorsal furrows are deep and distinct. The anterior border is narrow and separated by a well developed preglabellar field. The palpebral lobes are prominent ridges. The fixigenae are broadly triangular in outline and about the same width as the glabella (tr.). The posterior lateral border is narrow but prominent. The triangular pygidium, which is not articulated with the cephalon, conical, of 4 or 5 segments, all of which are separated by furrows; the conical axial lobe tapers slightly posteriorly; the flat to slightly convex pleural lobes are divided into 3 or 4 broad pleural bands; the marginal border is narrow and distinctly delimited by the marginal furrow; no marginal spines are preserved. The librigena is elongate, narrow, and crescentic, with a medium-sized genal spine.

The features which differentiated this stage from the earlier one are: the appearance of the preglabellar field, the axial separation of the glabellar furrows, and the change of the pygidial axis from hemicylindrical to conical.

Figured specimens. Metaprotaspides, U.C.M. 38736a-c.
Paraprotaspides, U.C.M. 38736d-h.
Early meraspides, U.C.M. 38736i-l, z.
Late meraspides, U.C.M. 38736m-r, v, w, a'.

Genus Acerocare Angelin, 1854

Acerocare ecorne Angelin

Pl. 13, figs. 1-34 and text-fig. 48.

Acerocare ecorne Angelin, N. P., 1878, pl. 25, fig. 10, p. 47; Mober, J. C., and Möller, H., 1898, pl. 10, figs. 1-10, p. 231; Henningsmoen, G., 1957, pl. 2, fig. 3, pl. 7, pl. 30, figs. 1-8, pl. 31, p. 243.

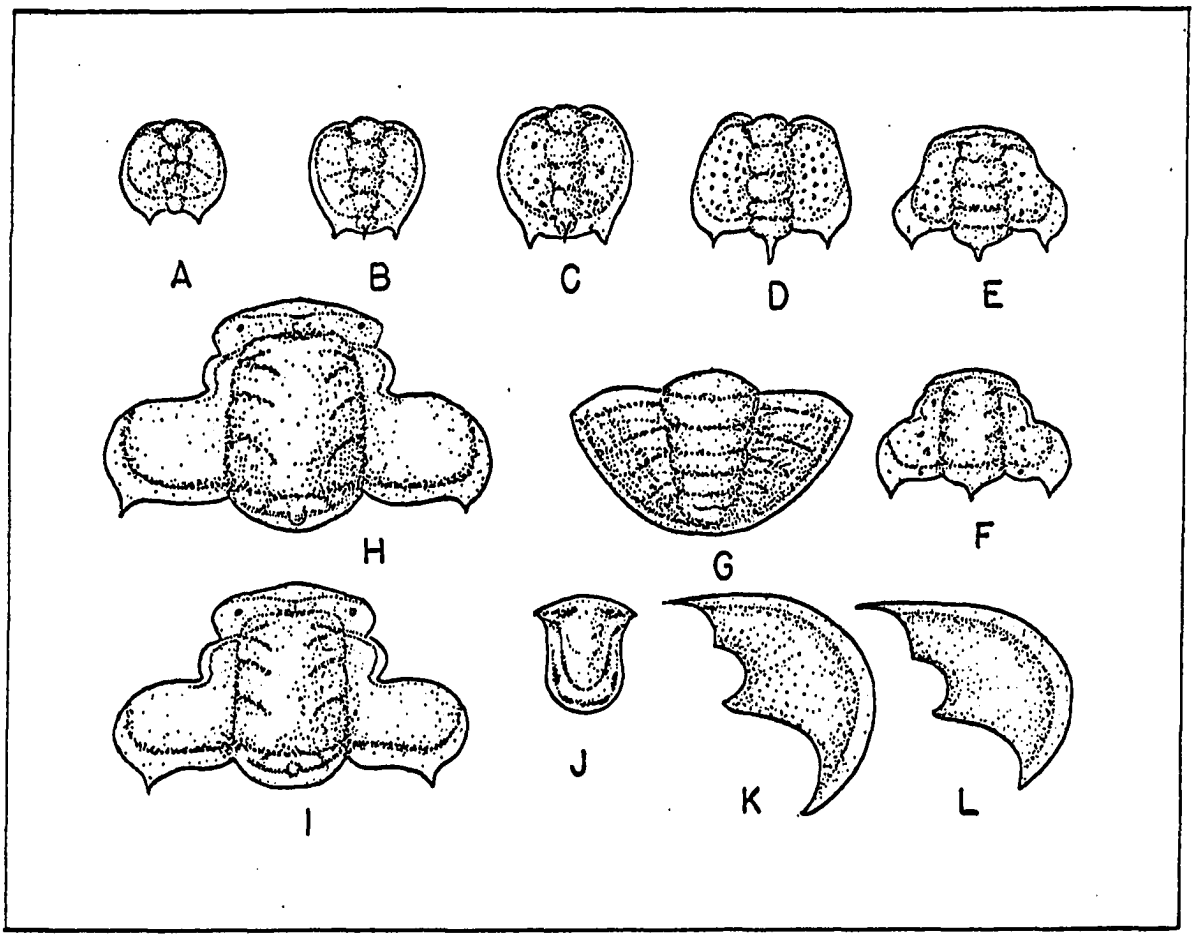
Diagnosis. Convex crandium bearing a broad subquadrate glabella and anteriroly situated palpebral lobes. Preglabellar field very narrow, limited by a narrow, subtriangular frontal border. Posterior fixigenae wide, bearing a pair of short spines at the posterior lateral border. The semi-circular librigena bearing a short, broad and rather curved terminal spine. Hypostoma elongate and occupied by an oval and convex median body. Subtriangular pygidium with 6 or more axial rings and a small terminal portion.

Cephalic surface covered by small granules; fine, radial ridges are present on the preglabellar field and ocular platform. A pair of distinct small nodes is present on the sides of the preglabellar field.

Acerocare ecorne Angelin, male?

Pl. 13, figs. 15,17,19,24,32,34, and text-fig. 48H, L.

Description. The cephalon is semi-circular in outline and wider (tr.) than long (sang.). The glabella is broadly subquadrate, marked by four pairs of glabellar furrows and a shallow anterior median pit. The dorsal furrow curves around the glabella and has a small median salient into the frontal margin of the glabella; at its mid-line of the



Text-fig. 48: A growth sequence of Acerocare ecorne Anglin. A, metaprotaspis, x 50; B,C, two paraprotaspides, x 56, x 47; D, early meraspis, x 32; E,F, two late meraspides, x 26, x 22; G, pygidium, x 6.8; H, "male" crandium, x 6.7; I, "female" cranidium, x 8; J, hypostoma, x 3.8; K, "female" librigena, x 7; L, "male" librigena, x 5. (Drawings from photographs.)

glabella (tr.) it is slightly expanded laterally. The crescentic occipital ring is marked laterally by a pair of curving furrows and medially by medium-sized spine or node. A median occipital ridge runs along the occipital ring (tr.). The narrow preglabellar field is limited by a fine, but well-defined frontal furrow. The anterior border is very narrow, slightly elevated and bluntly pointed anteriorly. The inter-ocular cheek is narrow. The small palpebral lobes are located far forward from the mid-line of the glabella (tr.). The posterior fixigenae are broad and transverse. The prominent and narrow posterior lateral border is deliminted by posterior lateral furrows, which curve anterior-laterally. A pair of short fixigenal spine is borne at the lateral margin of the posterior lateral border.

The librigena is semi-circular in outline and gently convex. The ocular platform is broad. The convex lateral border is of medium width and defined by a shallow and broad lateral furrow. The anterior and posterior ends of the librigenae are sharply pointed.

The pygidium is subtriangular in outline. The conical axial lobe tapers posteriorly, is divided into 4 or 5 axial rings and a small terminal portion. The dorsal furrow is deeply impressed anteriorly and shallow around the posterior margin. The pleural lobes are slightly narrower than the axis (tr.), gently convex, and down-sloping to the narrow margin; the 4 or 5 pleural bands are all marked by broad, concave pleural furrows; the faint interpleural grooves are oblique to the pleural furrows.

The surface of the skeleton is covered by fine granules, and irregular ridges are developed around the margin of the pygidium.

Figured specimens. Crandia, U.C.M. 38738n, p, r.
Librigena, U.C.M. 38738w.
Pygidia, U.C.M. 38738e', g'.
Hypostoma, U.C.M. 38738t.

Acerocare ecorne Angelin, female?

Pl. 13, figs. 13,14,16,18,25,30,31,33 and text-fig. 48I, K.

Comparison. The glabella of the presumed female form is narrower, longer and more cylindrical than that of the male form; the librigena is longer and narrower; and the pygidium is triangular. The sexual ratio is 115.

Horizon and Locality. Upper Cambrian, Acerocare zone ($2d_a$), Nye, Joukoping, Sweden.

Figured specimens. Crandia, U.C.M. 387381, m, o, q.
Librigena, U.C.M. 38738x.
Pygidia, U.C.M. 38738c', d', f'.

Acerocare ecorne, Angelin, ontogeny

Metaprotaspid stage (Pl. 13, figs. 1-2 and text-fig. 48A). The shield is rounded to subrounded, convex, and about 0.20-0.29 mm. in length (sag.). The marginal border of the shield is narrow and has a pair of short and broad spines projecting posteriorly from the posterior-lateral border. The fusiform axis is about the same width as the pleural lobe (tr.) and is delimited by dorsal furrows. It is composed of a frontal lobe, two pairs of axial nodes and two terminal rings. The paired anterior pits are distinctly marked in the anterior

lateral margin of the frontal lobe. The palpebral ridges and the palpebral lobes are indistinct. The surface of the shield is covered by fine granules.

Paraprotaspid stage (Pl. 13, figs. 3-6 and text-figs. 48B, C). The subrounded, convex shield varies from 0.30-0.40 mm. in length (sag.), is surrounded by narrow marginal border. The fusiform axis is the same width as the pleural lobe and is divided into five convex, well defined rings. The rings are connected by a very narrow ridge along the median axis (sag.), and the small terminal ring bears a minute median spine. The convex frontal lobe is semicircular in outline and bears a pair of elongate pits on the anterior lateral portion. The distinct palpebral ridges extend laterally from behind the anteiror pits to the lateral borders. The extreme ends of the borders are arched posteriorly and laterally and bear a pair of sharp-pointed spines. A small triangular protopygidium, which possibly consists of only one segments, is curved ventrally between the posterior spines from the posterior cephalic margin. The surface is covered by moderately large granules.

This stage differs from the preceding one in that here the axial nodes are fused to form five complete rings and the protopygidium first appears.

Early meraspid stage (Pl. 13, figs. 7-9, 26 and text-fig. 48D). The cranidium is trapezoidal in outline about 0.40-0.70 mm. in length (sag.), and the cranidium is disassociated from the pygidium. The fusiform glabella may be slightly expanded anteriorly, and is composed of five distinct axial rings. The terminal or occipital ring is smaller than the preceding rings and bears a medium-sized median spine. The

palpebral ridges and the palpebral lobes are situated at the anterior lateral margin of the shield. The posterior fixigenal borders are expanded laterally, and bear a pair of spines directed posterior-laterally from the lateral borders. The facial sutures are obscure but may be located at the anterior-lateral corners of the cranidium, as is suggested by the palpebral lobes and the posterior fixigenal borders.

The pygidium is elongate-triangular in outline and slightly convex; its axial lobe is slenderly conical, tapering posteriorly and divided into four rings, but some of which may be thoracic segments. The pleural lobes are convex above the dorsal furrow, and each segment projects marginally as a pair of short, broad spines. The surface is regularly ornamented with large granules.

In this stage the instars differ from the paraprotaspides in that the shield assumes a trapezoidal outline and the posterior fixigenal border becomes laterally expanded.

Late meraspid stage (Pl. 13, figs. 10-12,20,22,27-29, and text-fig. 48E, F). The cranidium is trapezoidal in outline and about 0.60-0.80 mm. in length (sag.). The subconcial glabella is slightly expanded at the mid-line (tr.) and divided by three pairs of complete furrows. The crescentic occipital ring is smaller than the glabellar rings; it arches posteriorly and bears a small median tubercle. The anterior border is narrow, convex, and curves anteriorly. The fixigenae are broad posteriorly and narrow anteriorly; the distinct palpebral lobes and ridges are located at the anterior-lateral corners of the crandium; the posterior fixigenal borders are deliminted by furrow and

curve anteriorly and laterally before reaching the margin; a pair of short spines projects from the posterior-lateral margins. The convex hypostoma is subquadrate in utline, with rounded posterior marginal border; its median body is small, subtriangular and convex; the posterior lobe is wide, convex, and U-shaped. The flat pygidium which is subtriangular in outline, has a slenderly conical axial lobe; the axial lobe is divided into 5 or 6 rings; the pleural lobes are about the same width as the axis and marked by 3 or 4 distinct pleural bands; the marginal border is narrow and no marginal spines are preserved. The surface is covered by medium-sized granules.

This stage is characterized by a subconical glabella, incomplete glabellar furrows, and a narrow anterior border; the hypostoma has a small median body and a broad posterior lobe; the pygidial axis is slenderly conical; and the librigenae have a narrow platform.

Figured specimens. Metaprotaspides, U.C.M. 38738a-b.
Paraprotaspides, U.C.M. 38738d-f.
Early meraspides, U.C.M. 38738g-i, y.
Late meraspides, U.C.M. 38738h-k, s, u.

Genus Highgatella Show, 1955

Highgatella facila, n. sp.

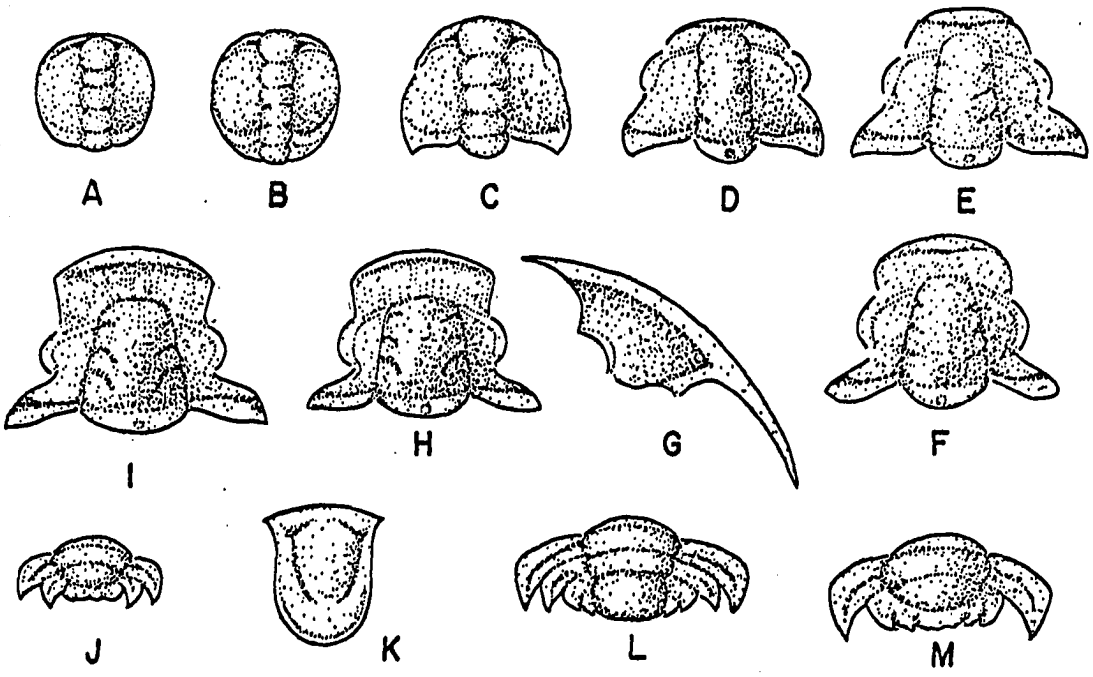
Pl. 15, figs. 1-26 and text-fig. 49

Diagnosis. Cranidium trapezoidal to subquadrate in outline, moderately convex. Glabella truncate-conical, marked by three pairs of glabellar furrows. Preglabellar field about one-half the length of glabella. Anterior border narrow. Fixigenae narrow. Eyes medium-sized and located at mid-line of glabella. Posterior lateral fixigena triangular. Dorsal furrow deeply marked. Librigena having medium-wide ocular platform and genal spine. Hypostoma subquadrate, with a large, convex median body. Pygidium oval, convex with two pairs of marginal spines and same number of axial rings; pleural lobe narrower than axis and having distinctly impresssed pleural furrow.

Highgatella facila, n. sp. male?

Pl. 15, figs, 13,14,17,20,21,23,25,26, and text-fig. 49H, L.

Description. The cranidium is trapezoidal in outline and convex in profile. The glabella is broadly conical with a slightly rounded frontal margin, three pairs of well defined glabellar furrows; the first pair of glabellar furrows, which are opposite the palpebral ridges, is short and porrly impressed; the second pair of glabellar furrows is deeper and extends a short distance behind the palpebral ridge; the last pair is longer and distinctly marked. The dorsal furrow is narrow and deep. The occipital furrow is shallow but well marked, deep laterally and shallow across the axial line (sag.). The crescentic occipital ring bears a median node. The preglabellar



Text-fig. 49: A growth series of Highgatella facila, n. sp. A, a metaprotaspis, x 62; B,C, two paraprotaspides, x 53; D, early meraspis, x 40; E, late meraspis, x 30; F, an early holaspid cranidium, x 14; G, librigena, x 5; H, "male" cranidium, x 10; I, "female" cranidium, x 9; J, immature pygidium, x 30; K, hypostoma, x 24; L, "male" pygidium, x 25; M, "female" pygidium, x 12. (Drawings made from photographs.)

field is one-third as long as the glabella, slightly convex and curves abruptly into the anterior furrow, which is narrow, distinct and arches anteriorly. The rounded and arched anterior border is narrow, being about one-fourth as wide as the preglabellar field. The fixigenae are narrow and flat, approximately one-fourth as wide as the glabella. The prominent eye-ridges extend from the anterior edges of the palpebral lobes medially to the dorsal furrow just behind the anterior lateral corner of the glabella; the medium-sized palpebral lobes are located on, or slightly forward from the mid-line of the glabella; the posterior fixigenae are triangular, convex, sloping down from the dorsal furrow to the impressed posterior-lateral furrows; the narrow posterior border is about two-thirds the length of the occipital ring. The anterior facial sutures are slightly divergent to parallel; the posterior facial sutures are divergently sinuous and cut the posterior lateral border with a sharp angle.

Libringena is convex, with a medium-wide ocular platform; the lateral furrow is shallow and broad; the lateral border is of medium-width, convex, and slopes gently down to the outer margin; the genal spine is slender and of medium length.

The pygidium is oval, transverse, and convex; the axial lobe is broad and convex above the pleural lobes and divided into two axial rings and a long terminal portion; the pleural lobe is narrower than the axis and marked by two pairs of pleural furrows; the marginal border bears two pairs of short, broad spines, which extend continuously from the pleural segmental tips.

The surface of the skeleton is covered by fine granules; radial

ridges are present on the preglabellar field, and a row of distinct pits is present along the cephalic marginal furrow.

Figured specimens. Paratype, Crandia, U.C.M. 38740n, m, q, r.
Librigenae, U.C.M. 38740w, x.
Hypostoma, U.C.M. 38740s.
Pygidium, U.C.M. 38740u.

Highgatella facila, n. sp. female?

Pl. 15, figs. 12,15,16,18,19,22,24, and text-fig. 49I, M.

Comparison. The cranidium of the female differs from that of the male by having a narrower and longer glabella, wider preglabellar field, broader pygidial axis with two axial rings and narrower pleural lobes.

Remarks. This species is represented by 20 mature and 50 immature specimens, which show a continual growth sequence. The largest female cranidium is about 20 mm. long and the male cranidium is about 15 mm. (sag.). The matrix material is light-brownish, medium-crystalline limestone. This species is distinguished from the type species H. gelasinata (Show) (1951, 1955) by its larger and more posteriorly located palpebral lobes.

Recently Winston and Nicholls (1967) assigned Lochman's (1964) Euloma cordilleri from the Williston Basin to Highgatella. The assignment is doubtful. Dr. Lochman's specimens were prepared by the writer while serving as her research assistant; at that time a detailed comparison was made among three closely similar genera, Euloma, Highgatella, and Parabolinella. The differences are: Euloma has a quadrate

cranidium, conical glabella, and deeply marked dorsal furrow; whereas Highgatella and Parabolinella have a trapezoidal to subquadrate cranidium, broadly subquadrate glabella, and shallower dorsal furrow. Moreover the preglabellar field of Euloma has a strongly elevated median boss whereas this field in Highgatella and Parabolinella has none. They are clearly different, but unfortunately, the specimens which were figured by Lochman are not all identical. The specimens which she shows on her pl. 63, figs. 27-30, 32-34, 36-38 (U.S.N.M. 140714, 140715a, c-f, h-j) are typical Euloma, whereas her fig. 31 (U.S.N.M. 140715b) is either a member of Highgatella or Parabolinella, and fig. 35 (U.S.N.M. 140715g) is a juvenile pygidium of Symphysurina with a peeled surface. These differences are easily discernible. Winston and Nicholl's (1967) specimens on their pl. 13, figs. 8,11,13 (Ut 12651-12653) are closely similar to Lochman's fig. 31 (U.S.N.M. 140715b) and appear to belong to Highgatella or Parabolinella, whereas Lochman's specimens are referable to Euloma, except for her pl. 63, figs. 31 and 35 (U.S.N.M. 140715b and 140715g). This conclusion was reached after comparison of present materials with Dr. Lochman's duplicates and topotypes(?) of Euroma ornatum Angelin, from Tremadocian Ceratopyge limestone, Bjerkasholmen, Norway, which were collected by Dr. K. E. Caster during a field trip of the International Geological Congress, 1962.

Horizon and Locality. Deadwood Formation, Missisquia zone, Lower Ordovician. Sheep Mt., Sundance, eastern Wyoming.

Figured specimens. Holotype, Cranidium, U.C.M. 38740.

Paratype, Cranidia, U.C.M. 38740lo, p.

Pygidia, U.C.M. 38740t, v.

Highgatella facila, n. sp. ontogeny

Metaprotaspid stage (Pl. 15, figs. 1-5 and text-fig. 49A). The spherical to subspherical shield is about 0.26-0.30 mm. in length (sag.) and distinctly divided into axial and pleural lobes by the dorsal furrow. The axial lobe is fusiform, tapering slightly anteriorly and posteriorly, and lacking distinct rings or ring-furrows. The anterior pits are faint; the frontal lobe tapers continuously from the axial lobes; the last axial, or occipital, ring is oval, transverse, and convex. No protopygidium is seen from the dorsal view. The surface is covered with fine granules.

Paraprotaspid stage (Pl. 15, fig. 6, and text-fig. 49B, C). The cranidium varies from 0.35-0.40 mm. in length (sag.), is trapezoidal in outline with a rounded anterior margin. The axial lobe is fusiform to cylindrical and divided into 5 rings by faint ring furrows; its frontal lobe is large and rounded; the occipital ring is distinctly separated by a deep occipital furrow and arches posteriorly. The faint and elongate anterior pits are located at the anterior lateral margin of the frontal lobe; a pair of short supercilioid ridges extends laterally from the anterior lateral margin of the frontal lobe. The pleural lobes are about one and one-half the width of the axial lobe. No protopygidium is associated with the cranidium. The surface is finely granulose.

The distinction from the metaprotaspid stage lies in the paraprotaspids having the cranidium trapezoidal in outline, and the axial

lobe cylindrical with defined ring-furrows.

Early meraspid stage (Pl. 15, figs. 7-9 and text fig. 49D). The convex cranidium is trapezoidal in outline and varies from 0.40-0.60 mm. in length. The glabella is cylindrical to anteriorly tapered and bears three pairs of glabella furrows. The dorsal furrow is deep and narrow. The occipital ring is crescentic and convex, possibly bearing a median tubercle. The narrow anterior border appears in contact with the frontal margin of the glabella; the anterior furrow is well defined and bends backward at the mid-point of the frontal glabellar margin (sag.). The broadly triangular fixigenae are of the same width as the glabella. The elevated palpebral lobes are located at the anterior one-third of the glabellar length, and are defined by distinct palpebral furrows. The posterior fixigenal border is twice as wide as the glabellar base, and divided by a wide and deep posterior-lateral furrow. The facial sutures converge anterior-medially to form a trapezoidal cranidium. The surface is covered with numberous small granules and occasionally large ones.

The distinctive characteristics of this stage are the conical glabella with three pairs of glabellar furrows and the development of the anterior border.

Late meraspid stage (Pl. 15, figs. 10-11 and text-fig. 49E). The convex cranidium is trapezoidal in outline and varies from 0.65 to 0.90 mm. long (sag.). The slenderly conical glabella is marked by three pair of well defined glabellar furrows. The dorsal furrow is narrow and deeply marked. The convex occipital ring is distinctly separated by an occipital furrow and bears a small median node. The

preglabellar field appears, slightly depressed in front of the preglabellar area. The narrow and convex anterior border is defined by an anterior furrow which curves slightly inward to form a median notch. The fixigenae are about one-third as wide as the glabella (tr.) and bear prominent palpebral ridges; the small crescentic palpebral lobes are deeply separated by palpebral furrows. The posterior fixigenal borders are triangular and of the same width as the glabellar base (tr.). The surface is generally covered by numerous fine granules and scattered large granules are seen on the fixigenae.

This stage differs from the earlier one in that the preglabellar field first appears, the fixigenae become narrow, and the palpebral lobes have moved posteriorly. The meraspis differs from the holaspis in having the glabella slenderly conical and the posterior lateral fixigenae wider. The glabella of the holaspid is truncate-conical; the posterior fixigenae are narrower; and preglabellar field is wider.

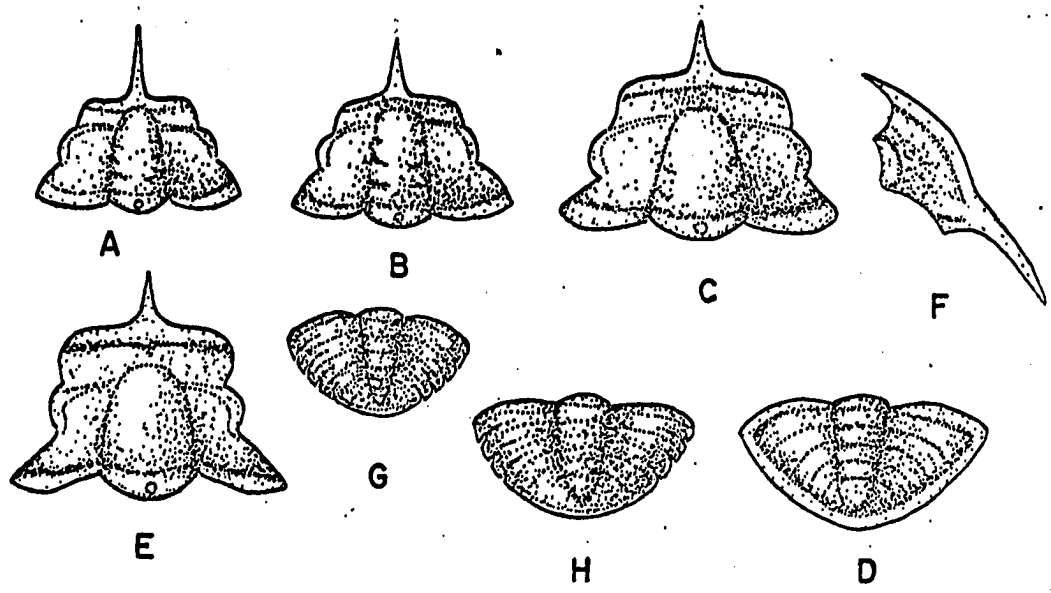
Figured specimens. Metaprotaspides, U.C.M. 38740a-d, e.
Paraprotaspis, U.C.M. 38740f.
Early meraspides, U.C.M. 38740g-i.
Late meraspides, U.C.M. 38740j, k.

Family Leiostegiidae Bradley, 1925

Genus Kepisis, n. gen.

Diagnosis. Cranidium trapezoidal in outline, convex; glabella conical with three pairs of rather distinctly impressed glabellar furrows; dorsal furrow shallowly impressed; preglabellar field of medium width; anterior border convex, same width as preglabellar field, with a stout median spine. Fixigenae about one-half the width of the glabella; palpebral lobe small, situated at the mid-line of the cranidium (tr.). Anterior facial suture lines convergently convex; posterior facial sutures divergent and straight. Librigenae with convex ocular platform and long genal spines. Pygidium transversely subtriangular, convex, divided into 5 or 6 segments; pleural lobes about twice as wide as axis; marginal border narrow, flat, and without spines.

Description. The cranidium is regularly trapezoidal in outline and moderately convex. The glabella is conical, with three pairs of very faint, obliquely directed glabellar furrows; the dorsal furrows are shallow and broad, but well defined; the occipital furrow is narrow, steep-sided and shallow across the center; the occipigal ring is crescentic, convex, curving backward, and bearing a tiny median tubercle. The preglabellar field is one-fourth as long as the glabella, gently deflected toward the anterior furrow; the anterior furrow, which has a median notch directed toward the preglabellar field, is deep laterally but shallow across the axis; the anterior border is convex, about the same width as the preglabellar field, and bearing a median spine. The fixigenae are flat to gently convex and about



Text-fig. 50: Kepisis stenotoides (Metthew), n. gen. A, an early meraspis, x 17; B, late meraspis, x 13; C,E, two holaspid cranidia, x 11, x 5.5; F, a librigena, x 1.7; D,G,H, a growth series of pygidia, x 11, x 25, x 16. (Drawings from photographs.)

one-half as wide as the glabella; the palpebral lobes are small and narrow and indistinctly separated by palpebral furrows; the faint palpebral ridges extend laterally, and gently arch forward; the posterior fixigenae are broad and triangular, with the border wider than the occipital ring.

The librigenae are moderately narrow and elongate with a long genal spine. The convex ocular platform is of medium width. The lateral border is moderately narrow, convex, and well delimited by a lateral furrow. The lateral and posterior furrows are not joined at the genal angle.

The pygidium is subtriangular, transverse, and convex. The axial lobe is cylindrical, slightly tapering posteriorly and ending before reaching the inner marginal furrow. Five axial rings are distinctly recognizable. The pleural lobes are broader than the axis, slightly convex, and well defined by a narrow and flat marginal border. Five pleural bands are divided by pleural furrows, the interpleural grooves being rather faint; the marginal border lacks spines.

Remarks. There are not very many trilobites which have a cranidium with a median spine at the anterior border. Acrocephalites, Shantongia, Dokimocephalus, Thysanopyge, Zuninaspis, Nascocephalus, Lonchodomas, and the dalmanitoids have this feature, but their other characteristics are quite different from those of Kepisis; e.g., the shape, position, and origin of the anterior spines of these forms are dissimilar. For example, in Shantongia and some dalmanitoids the spine is developed from the rostral plate; in Lonchodomas and some other dalmanitoids the spine is developed from the anterior glabella. In Nascocephalus, Dokimocephalus,

and Acrocephalus it is, however, located at the anterior border, but the shape of the cranidia and spines are completely different in form. The present form has no generic features which could associate it with any of the anteriorly spinose genera so far known.

The present genus is very similar to Chuangia and Anomocarella, except that these two genera have no anterior border spine and possess wider posterior fixigenae and less numerous pygidial segments. On the other hand, Chuangia, Anomocarella, and Kepisis have some features in common: the shape of the cranidium and the glabella, the convexity, dorsal furrow, and outline of the pygidium are all closely similar in these three genera. Therefore, the present genus Kepisis could be a member of either the Asaphiscidae or Leiostegiidae. Age considerations would incline one to prefer the latter family assignment. It should be pointed out that Kepisis shows affinities relating it to the Asiatic realm of Cambrian time.

Type species. Kepisis stenotoides (Matthew), n. gen.

Kepisis stenotoides (Matthew), n. gen.

Pl. 6, figs. 1-14 and text-fig. 50

Anomocare stenotoides Matthew, G. F., 1898, p. 139-141, pl. 2, figs. fa-i.

Remarks. This species is represented by 15 cranidiia, 3 librigenae, 8 pygidia, and a few thoracic segments, all prepared from a single piece of dark-grey, finely crystalline limestone. The material was found in the Geology Museum, University of Cincinnati, labeled as "Kennebec River, St. John, N. B.". However, no stratigraphic horizon,

detailed locality or identification are given. Drs. F. Rasetti and B. F. Howell, who are familiar with the geology and paleontology of the New Brunswick area, suggest that the specimens in question may belong to Anomocare stenotoides, published by Matthew in 1898. Dr. Rasetti reported that Matthew's types at the Royal Ontario Museum are quite similar to the present material. Dr. Howell, on the other hand, says that he has collected thousands of trilobites from the St. John region, but never found any form like the present one. It is his thought that the present forms are a new genus and quite possibly belong to the Upper Cambrian. Through the courtesy of the Royal Ontario Museum, Matthew's types were loaned for comparison with the present material. The specimens are lithologically and morphologically identical and were quite probably collected from a same general region and horizon.

Horizon and Locality. Probably Bretonian (Upper Cambrian or Lower Ordovician), Kennebec River, St. John, N.B., Canada.

Figured specimens. Cranidia, U.C.M. 38730f, and 38730.
Librigena, U.C.M. 38730g.
Pygidia, U.C.M. 38730m.
Thoracic segment, U.C.M. 38730h.

Kepisis stenotoides (Matthew), n. gen., ontogeny

Early meraspid stage (Pl. 6, figs. 1,2,10,11 and text-fig. 50A). The cranidium is about 1.0-1.22 mm. in length (sag.), trapezoidal in outline, convex, with distinctly impressed dorsal furrows. The slenderly conical glabella tapers forward with a rounded anterior margin and has three pairs of very weakly marked glabellar furrows. The

crescentic occipital ring curves posteriorly and bears a tiny median node. The narrow anterior border is sharply defined by a wide, concave anterior furrow and bears a long, slender, anterior projecting, median spine. The fixigenae are fairly convex, slightly wider than the glabella, with a pair of elongate sickle-shaped palpebral lobes which approach the glabella at one-third the distance from its front margin. The posterior fixigenal borders are convex, broad, and slightly geniculate. The posterior lateral furrows are broad laterally with a narrow, convex marginal border. The short anterior branches of the facial sutures are convergent; the posterior branches are divergent or slightly transverse.

The convex pygidium is triangular in outline. The axis is slender, tapering posteriorly, convex above the pleural lobes, and divided into at least eight axial rings by transverse furrows. The pleural bands, which slope gently downward to the margins, are well defined by pleural furrows and end with short spines; no marginal borders have been observed.

The surface is covered by fine granules.

Late meraspid stage (Pl. 6, figs. 3-5,12,13 and text-fig. 50B). The cranidium is convex, trapezoidal in outline, and varies from 1.30 to 1.80 mm. in length (sag.). The conical glabella is weakly marked by three pairs of broad, posterior-laterally directed glabellar furrows. The occipital furrow is distinctly marked and delimited by a crescentic, posteriorly arching occipital ring which as a minute median tubercle. The preglabellar field is axially flat, but deflected laterally. The narrow anterior border arches forward, with an anteriorly

projecting median spine. The anterior furrow is steep-sided but shallow across the axis. The fixigenae are wider than the glabella and bear a pair of small palpebral lobes which are located slightly in front of the mid-line of the cranidium (tr.), and connect with a pair of prominent palpebral ridges. The anterior facial sutures are divergently convex, and the posterior ones are divergently straight. The pygidium is composed of 8 to 14 segments and is subtriangular to semi-oval in outline; its marginal border is narrow and bears numerous short spines. One specimen (fig. 12) shows a pygidium with at least two articulating thoracic segments.

The surface is finely granulose, and well defined radial ridges are present on the preglabellar field.

The morphologic changes during ontogeny are as follows: the anterior border spine changes from long to short; a preglabellar field is progressively developed; the initially long slender glabella becomes progressively short and broad; wide fixigenae become narrow; the palpebral lobes migrate from the anterior lateral margin to the mid-length of the cranidium; and the pygidial axis changes from slenderly conical to almost cylindrical, with nearly parallel dorsal furrows; the spiny pygidial margin becomes smooth.

Figured specimens. Early meraspides, U.C.M. 38730a, b, i, j.
Late meraspides, U.C.M. 38730c-e, k, l.

Family Missisquoiidae Hüpe, 1959

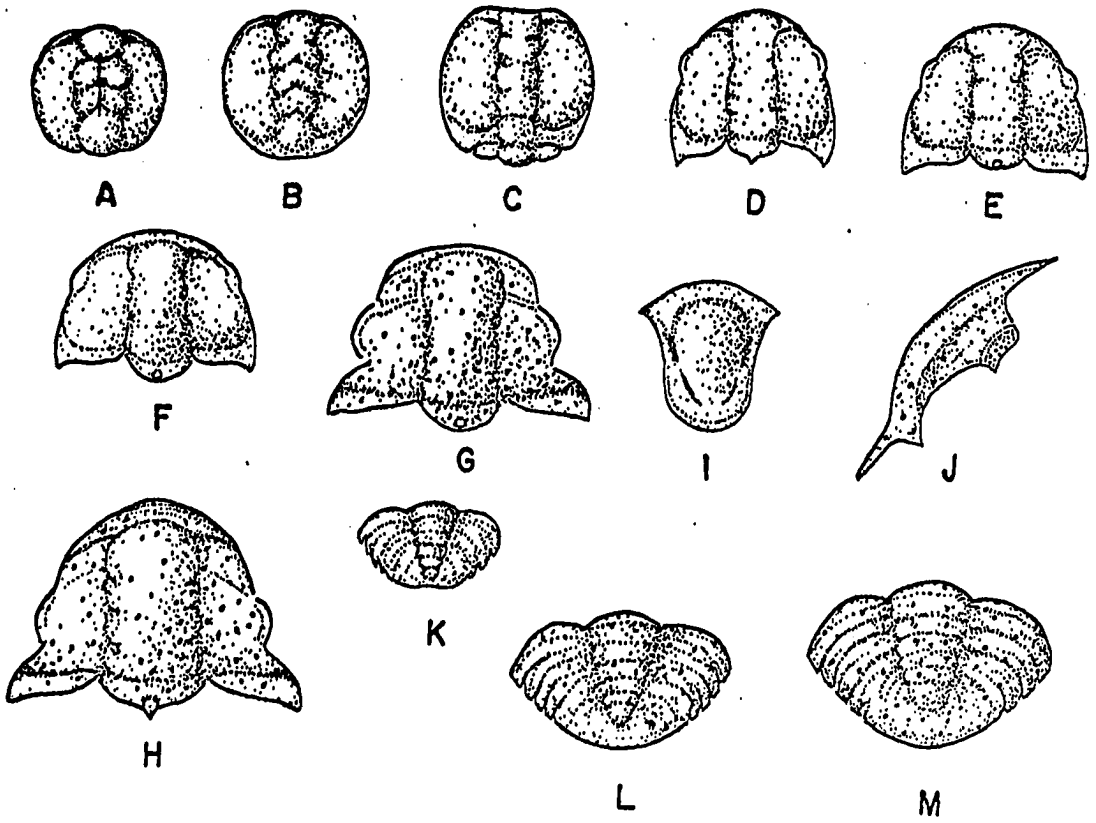
Genus Missisquoia Show, 1951

Missisquoia cyclochila, n. sp.

Pl. 14, figs. 1-28 and text-fig. 51

Diagnosis. Cranidium triangular in outline, convex. Glabella parallel-sided to slightly expanding both anteriorly and posteriorly, with two pairs of distinct glabellar furrows. Dorsal furrow deeply impressed. Eye small, located behind mid-line of the glabella (tr.). Fixigena about one-half as wide as glabella. No preglabellar field. Anterior border convex, arching forward. Librigena narrowly elongate, having a short genal spine. Pygidium semi-circular, convex, with 6 or 7 axial rings and a small terminal portion.

Description. The small cranidium is triangular in outline. The convex glabella is parallel-sided or slightly expanded both anteriorly and posteriorly, with a rounded frontal margin and small median notch. Three pairs of glabellar furrows are seen; the first pair is faint, the second and third ones are deeply impressed and extend posterior-laterally from the dorsal furrows. The dorsal furrow is moderately deep at the mid-line of the glabella but becomes shallower both anteriorly and posteriorly. The occipital furrow is distinct, shallow across the central axis and deeper laterally; the crescentic occipital ring is widest at its center and tapers laterally; a minute node is borne on the center of the ring. No preglabellar field is present; the anterior furrow is narrow and deeply marked; the anterior border is narrowly rounded and convex. The fixigena is convex and about one-half the width of the glabella; the small palpebral lobes



Text-fig. 51: A growth sequence of Missisquoia cyclochila, n. sp. A, anaprotaspis, x 70; B, metaprotaspis, x 70; C, paraprotaspis, x 62; D,E, two early meraspides, x 43, x 45; F, late meraspis, x 24; G,H, two holaspides, x 18, x 12; I, hypostoma, x 18; J, librigena, x 20; K,L,M, growth series of pygidia, x 50, x 28, x 19. (Drawings made from photographs.)

are located behind the mid-line of the glabella (tr.) and lack furrows; the palpebral ridge is faint, obliquely directed toward the anterior-lateral margin of the glabella. The posterior lateral fixigenae are broad, and convex; the posterior-lateral fixigenal borders are wide, about the same width as the occipital ring. The anterior branches of the facial sutures are straight and converge toward the anterior border; the posterior branches are divergently sinuous.

The hypostoma is subquadrate with a narrow marginal border and a large median body. Its lateral wings are short and broad.

The librigenae are moderately convex, narrow and elongate, with a short genal spine; the ocular platform is narrow and convex; the lateral border is broadly flat, of about the same width as the platform, and separated by a rather faint lateral furrow. The pygidium is semi-circular to triangular in outline and strongly convex; its conical, posteriorly tapering axial lobe consists of 6 or 7 axial rings and a terminal portion. The convex pleural lobes curve ventrally around the margin; the pleural furrows and interpleural grooves are well marked.

The surface of the skeleton is covered by fine to medium-sized granules; elevated and parallel ridges are present along the outside of the cephalic border.

Remarks. This species is represented by 15 mature and 45 immature specimens which show a continuous growth sequence. The largest cranidium is about 5.0 mm. in length (sag.), and the smallest immature specimens 0.22 mm. long (sag.). The material is from reddish-brown, medium to coarsely crystalline limestone.

This species differs from M. typicalis Show, (1951), M. nasuta Winston and Nicholls, and M. inflata Winston and Nicholls (1967) by its rounded anterior border, palpebral lobes located behind the mid-line of the glabella, librigena with short genal spine, pygidium without any marginal spines, and its pygidial axis not extending to the posterior pygidial margin.

It is interesting to note that the present genus is very similar to the genus Parakoldinoides Endo (1937), from northern China and southern Manchuria. These two forms are believed to be closely related; the pygidium referred by Endo to Parakoldinoides may have been misassociated.

Horizon and Locality. Lower Ordovican, Missisquoia zone, Deadwood Formation. South side of Sheep Mt., Sundance, eastern Wyoming.

Figured specimens. Holotype, Cranidium, U.C.N. 38749.
Paratype, Cranidia, U.C.M. 38749r.
Librigena, U.C.M. 38749t.
Hypostoma, U.C.M. 38749s.
Pygidia, U.C.M. 38749x, y.

Missisquoia cyclochila, n. sp., ontogeny

Anaprotaspid stage (Pl. 14, fig. 1, and text-fig. 51A). The spherical shield has a length of about 0.22 mm. (sag.). The fusiform axial lobe is composed of a medium sized frontal lobe, two pairs of oval notes, and a larger terminal tubercle. The frontal lobe is delimited by a pair of anterior pits; two pairs of central nodes are divided by a longitudinal fissure and transverse grooves; the large

terminal tubercle occupies about one-third the length of the axial lobe. The dorsal furrow is faint. The pleural lobe is convex and slightly narrower than the axial lobe. The surface is finely granulose.

Metaprotaspid stage (Pl. 14, figs. 2, 3, and text-fig. 51B). The convex shield is about 0.26-0.30 mm. long (sag.) and subspherical in outline. The fusiform to cylindrical axial lobe is distinctly defined by dorsal furrows; the frontal lobe is rounded, convex, with faint anterior pits; the three transverse axial rings are of subequal size, and the terminal tubercle is large, elongate, and convex. The pleural lobes are convex and slightly narrower than the axial lobe. The surface is covered by fine granules.

The important feature of this stage is that the shield is subspherical with five complete axial rings which are apparently formed by the fusion of the axial nodes.

Paraprotaspid stage (Pl. 14, figs. 4-7 and text-fig. 51C). The shield is subspherical, convex, about 0.35-0.55 mm. in length (sag.). The axial lobe is cylindrical to slightly fusiform with a larger frontal and three equal sized axial rings; the frontal lobe is delimited by furrows and anterior pits; a pair of supercilioid ridges extend lateral from the anterior-lateral margin of the frontal lobe. The dorsal furrows are distinctly impressed. The pleural lobe is approximately the same width as the axial lobe or slightly wider.

The protopygidium was not observed, but some specimens show a transverse ring behind the fifth axial ring,which suggests the pygidium, although its nature is unknown. The surface is covered by fine granules.

The distinct feature of this stage is the well developed posterior

lateral border.

Early meraspid stage (Pl. 14, figs. 8-15, 23 and text-fig. 51D, E, K). The subtriangular to trapezoidal cranidium ranges from 0.40 to 0.60 mm. long (sag.). The glabella is slenderly fusiform with a slightly expanded frontal lobe. The anterior pits are shallow impressed to almost absent in the larger specimens. The glabellar furrows are deep at the dorsal furrow and shallow across the central axis. The occipital furrow is well defined. The occipital ring is wide at the axial line (tr.), narrowing laterally and bearing a medium tubercle. The convex fixigenae are about one and one-half times as wide as the glabella. The posterior lateral fixigenae are broadly triangular, curve ventrally from the dorsal furrow, and extend posterior-laterally. The rear borders are of medium width, well impressed by a border furrow and terminate with a pair of projections. The facial sutures are only seen in the anterior-lateral corners of the cranidium. The triangular and convex pygidium bears 5 or 6 axial rings and a small terminal portion; the pleural lobes are separated into 5 or 6 pleural bands; they are convex, and curve ventrally toward the margin; the pleural bands terminate in short, broad marginal spines. The surface is finely granulose; possibly one or two articulating thoracic segments precede the meraspid pygidium.

The distinct features of this stage are the trapezoidal cranidium, broad and shorter glabella, the dorsal facial sutures, and expanded posterior-lateral borders.

Late meraspid stage (Pl. 14, figs, 16,17,24,25 and text-fig. 51F, L). The convex cranidium is trapezoidal in outline and about 0.70-

1.00 mm. (sag.) long. The glabella is cylindrical to slightly expanded at both the anterior and posterior ends; the glabellar furrows are faint. The dorsal furrows are deeply marked. The occipital furrow is narrow and distinct laterally; the crescentic occipital ring bears a minute tubercle. The anterior border is narrow, roundly arching forward, and delimited by the anterior furrow. No preglabellar field is observed. The fixigenae are of about the same width or slightly narrower than the glabella. The posterior-lateral fixigenae are convex, broad, and triangular. The palpebral lobes lack distinct palpebral furrows and are located at or slightly posterior from the mid-line of the glabella. The facial sutures extend from the posterior-lateral border convergently, forming a trapezoidal cranidium.

The semi-circular pygidium has a conical axial lobe which tapers backward to the posterior marginal border and is divided into 6 or 7 axial rings and a small terminal portion. The pleural lobes are composed of 5 or 6 pleural bands, all separated by pleural furrows, and bear interpleural grooves. The marginal border is sharply curved in a ventral direction. The surface is covered by medium-fine granules.

This stage is characterized by a subquadrate glabella, the narrow anterior border, and by having the pygidial axis extending to the posterior marginal border.

Figured specimens. Anaprotaspis, U.C.M. 38749a.
Metaprotaspides, U.C.M. 38749b, c.
Paraprotaspides, U.C.M. 38749d-g.
Early meraspides, U.C.M. 38749h-o, u.
Late meraspides, U.C.M. 38749p, q, v, x.

Family Encrinuridae Angelin, 1854

Genus Libertella, n. gen.

Diagnosis. Cranidium subtriangular to subtrapezoidal in outline, convex, having a pair of long fixigenal spines. Glabella strongly expanded forward without glabellar furrows. Fixigenae quadrate, broad posteriorly, occupied by a pair of small palpebral lobes. Librigenae narrow with steeply sloping ocular platform. Hypostoma diamond-shaped with a slightly convex median body. Thorax divided into at least eight segments; axis convex, elevated above pleural lobe, and bearing median spines. Pygidium subtriangular with five pairs of small marginal spines directed horizontally and three pairs vertically. Surface covered by large granules and spines.

Description. The cranidium is subtriangular in outline. The glabella is expanded forward, swollen above the fixigenae, and not marked by glabellar furrows; the dorsal furrow is deep and broad; the occipital furrow is deep, narrow, and steep-sided. No anterior border or preglabellar field are seen. The fixigenae are triangular in outline and bear a pair of long fixigenal spines; the palpebral lobes are small, rounded, prominent and situated on, or slightly behind, the mid-line of the glabella (tr.); the posterior fixigenae are broad and have narrow posterior borders; the posterior fixigenal furrows are narrow and distinct, and turn anterior-lateral before reaching the margin. The anterior branches of the facial sutures are convergent, the posterior nodes are divergently transverse. The surface is covered by medium sized granules and spines; there are four pairs of long vertical spines on the anterior half of the glabella; two pairs on the

palpebral lobes; one on the posterior center of the fixigenae; and at least five pairs inside the lateral border and fixigenal spines.

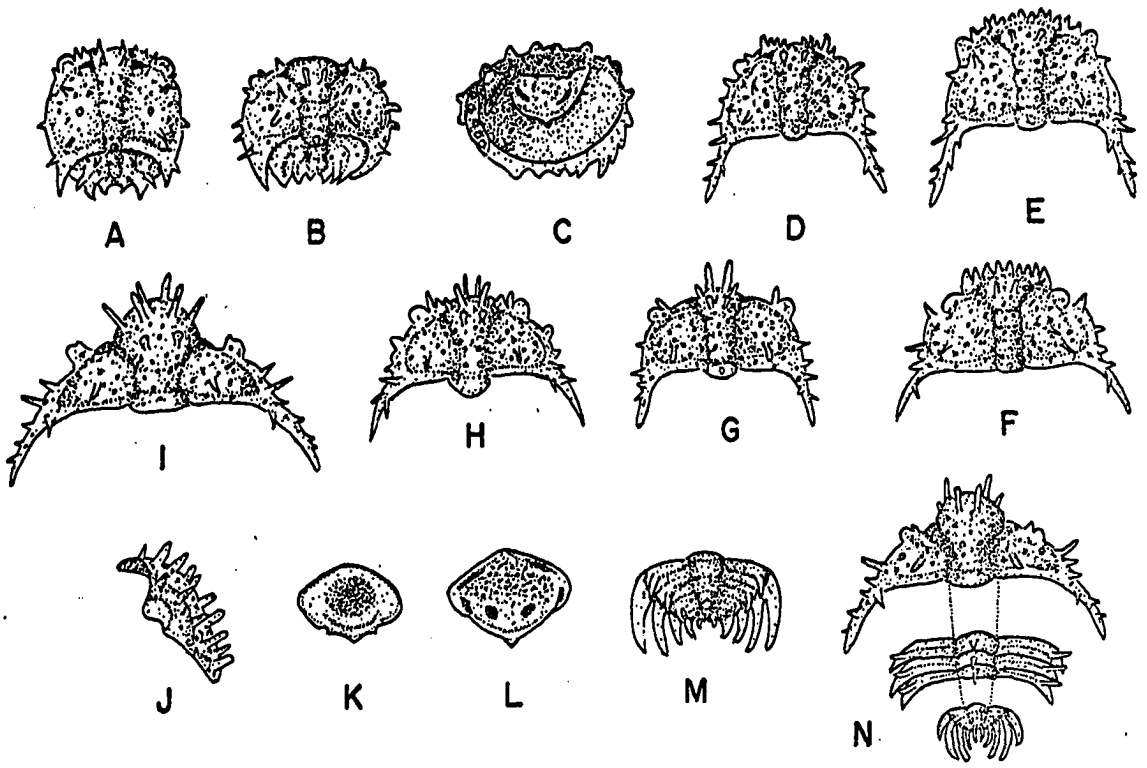
The librigena is triangular and has a rounded lateral border; no genal spine is present; the ocular platform is narrow; the palpebral ring is blunt and vertical. The surface is covered by granules. Numerous long and short spines extend from the lateral border.

The hypostoma is quadrilateral, with a low median body; the anterior margin is slightly acute; the lateral wings bear upturned narrow and tilted margins; the posterior margin is upturned and ridged, with a median spine directed posteriorly. The posterior-lateral areas are marked by a pair of distinct elongate nodes. The anterior half of the hypostoma is covered by coarse granules.

The thorax is divided into at least eight segments; the axis is convex above the pleural lobes, and each ring has a tiny median spine. The pleural lobes are moderately wide and curve ventrally; each segment bears a pair of long and short lateral spines on the outside half of the pleural bands. The surface is granulose.

The pygidium is semi-circular in outline; its axis is convex above the pleural lobes, which are flat and curve ventrally along the margin; the axis is divided into four rings and a small terminal portion; no tubercles are present; the four pleural segments each bear a pair of long posteriorly directed marginal spines and a pair of vertical spines on the margin.

Remarks. This genus resembles the genus Bevanopsis Cooper, (1953) but Libertella has a cranidium with less expanded glabella, no spines on the posterior fixigenal borders and occipital ring, and



Text-fig. 52: Libertella corona, n. gen. et sp. A-C, dorsal and ventral views of two paraprotaspides, x 38, x 35; D-F, three early meraspides, x 26, x 25, x 25; G,H, two late meraspides, x 18, x 16; I, adult cranidium, x 15; J, librigena, x 15; K, L, ventral and top views of two hypostomata, x 10; M, pygidium, x 33; N, reconstration, x 13. (Drawings made from photographs.)

fewer spines on the surface. Libertella differs from the genera Encrinurus Emmrich (1844), and Encrinuroides Reed (1931) in that Libertella has a spinose skeleton, whereas the other two genera have no spines; their pygidia are elongate-subtriangular. Doubtlessly, this genus is a member of the family Encrinuridae, because it has 1) proparial facial sutures, 2) a small palpebral lobe, 3) forwardly expanded glabella, 4) possesses no anterior border or preglabellar field, and 5) has a prominently ornamented skeletal surface.

Type species. Libertella corona, n. gen. et sp.

Libertella corona, n. gen. et sp.

Pl. 16, figs. 1-39 and text-fig. 52

Bevanopsis ulrichi Cooper, B., 1953, p. 32, pl. 13, figs. 23, 24 only. (not figs. 21, 22, 25).

Remarks. This species is represented by more than two hundred specimens, all etched from a few pieces of black, finely crystalline limestone. Both immature and mature forms are well preserved and a beautiful growth sequence obtained. The young skeletons resemble those of Calliops strasburgensis Ulich and Delo (194), but comparing the same-sized instars, the present species has a narrower axis and but little expanded frontal lobe, whereas C. strasburgensis has a wider axis and the frontal lobe is strongly expanded forward.

Cooper (1953) figured four cranidia referred to his Bevanopsis ulrichi. His figure 21 (the holotype, U.S.N.M. 116485a) is a moderately complete cranidium, showing a well preserved glabella and part of the fixigenae. The other four cranidia are all poorly

preserved specimens, but the glabellae are well shown and there is no doubt that the specimens of his figures 22, 25 (U.S.N.M. 116485b and 116485c) are identical to his holotype. On the other hand, his figures 23, 24 (U.S.N.M. 116485c and 116485d) are alike in all characteristics but are unquestionably synonymouse with the present species, L. corona.

Horizon and Locality. Lower Middle Ordovician, Edinberg Formation, 1.5 miles Southeastern Strasburg Junction, Virginia.

Figured specimens. Holotype, A complete skeleton, U.C.M. 38741.
Paratype, Cranidia, U.C.M. 38741o-q, d'.
Librigenae, U.C.M. 38741r-t.
Thoracic segment, U.C.M. 38741 u.
Hypostomata, U.C.M. 38741v, w.
Pygidia, U.C.M. 38741a'-c'.

Libertella corona, n. gen. et sp., ontogeny

Paraprotaspid stage (Pl. 16, figs. 1-4,7,8 and text-fig. 52A-C). The subspherical shield is about 0.45 to 0.48 mm. in length (sag.), with separated axial and pleural lobes. The anteriorly expanded axis is divided into five or six axial rings by faint furrows. The fixigenae are broad, convex, and approximately twice as wide as the glabella; the palpebral lobes are located at the anterior-lateral margin of the shield, and at a short distance from the lateral margin of the frontal lobe. The protopygidium is transverse, has one or two segments and a spinose margin.

The surface of the skeleton is covered by granules and scattered spines; three pairs of spines are located on the frontal lobe, of which

two pairs are directed forward from the anterior margin, and the other pair is on the sides of the base; seven pairs of spines occur on the fixigenae, of which three pairs are on the inner margin, additional pairs, including the large posterior fixigenal ones, extend laterally from the outer margin. A tiny median tubercle occurs on the occipital ring, and three pairs of tubercles are distributed along the posterior protopygidial margin.

The underside of the shield has a narrow doublure along the posterior margin; the hypostoma is semi-circular with a few pairs of marginal spines; the librigena is subtriangular and narrow with a spinose lateral margin.

Early meraspid stage (Pl. 16, figs, 5,6,9-11 and text-fig. 52D-F). The trapezoidal cranidium ranges from 0.40-0.55 mm. in length (sag.). The glabella is expanded anteriorly and separated into four rings by faint, transverse furrows; the dorsal furrows are distinct; the broad occipital ring is defined by a distinct occipital furrow and bears a median tubercle. The fixigenae are twice as wide as the glabella at the mid-line of the cranidium (tr.); the small palpebral lobes are located in front of the first glabellar furrow (tr.); the fixigenae are broad with rounded, gently deflected lateral margins; the posterior fixigenal border is narrow and delimited by a furrow; a pair of long fixigenal spines projects posteriorly from the hind border; the skeletal surface is covered by large granules and spines. The latter are arranged as in the previous stage, but have small and shorter spines appearing among them.

There are no striking morphologic changes between the present

stage and the previous one, except for the displacement of the pygidium, increase in the number of smaller spines, and the posterior-lateral migration of the palpebral lobes.

Late meraspid stage (Pl. 16, figs. 12-16,25,26,28-31 and text-fig. 52G, H). The cranidium is subtrapezoidal, convex, and about 0.60-1.00 mm. in length (sag.). The glabella is expanded slightly anteriorly, with two pairs of steep-sided glabellar furrows; the occipital ring is broad, elevated and distinctly delimited by the occipital furrow. The fixigenae are more than twice as wide as the glabella at the mid-line of the cranidium (tr.); the small palpebral lobes are small, imbricated, and situated slightly behind the glabellar expansion (tr.); the posterior fixigenal furrows are narrow, distinct, and turn anteriorly before reaching the lateral borders; the posterior fixigenal borders are narrow and continue as a pair of long and posterior-laterally directed fixigenal spines.

This stage is distinguished from the previous one in that the number of smaller cranidial spines is reduced; the palpebral lobes have shifted posteriorly from the anterior-lateral margin; the hypostoma bears three pairs of posterior marginal spines; and the pygidium is possibly associated with 2 thoracic segments (figs. 28,29).

Figured specimens. Paraprotaspides, U.C.M. 38741a-c, f.
Early meraspides, U.C.M. 38741d-g, h, i.
Late meraspides, U.C.M. 38741j-n, x-z.

Family Proetidae Salter, 1864

Genus Phaseolops Whittington, 1963

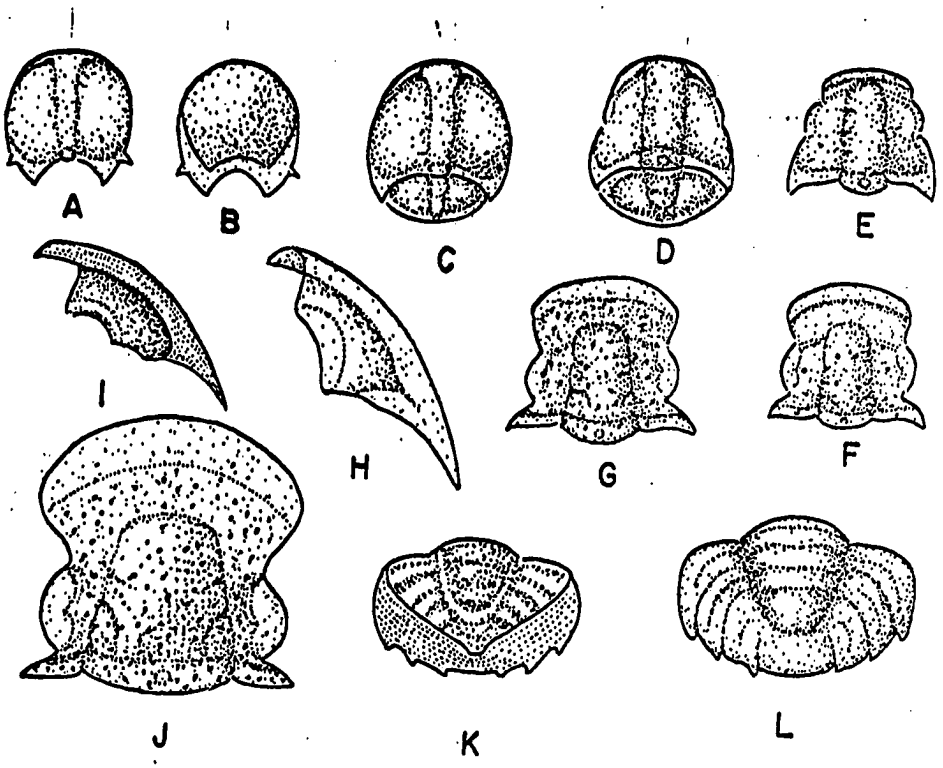
Phaseolops conus, n. sp.

Pl. 17, figs. 1-31, and text-fig. 53

Diagnosis. Cranidium subquadrate, convex. Anterior border rounded, arching forward. Glabella conical, last pair of glabellar furrows deeply marked. Dorsal furrow deeply impressed. Occipital ring convex, bearing a tiny median tubercle. Preglabellar field very broad, having a very distinct anterior furrow. Fixigenae very narrow. Palpebral lobe medium-sized, and located behind the mid-line of the glabella. Posterior fixigenae narrow. Librigenae elongate, having a medium-sized genal spine. Pygidium convex, widely subtriangular in outline, with three distinctly divided pygidial segments, each segment ending with a pair of short, broad, posteriorly directed spines.

Surface covered by large and small granules, parallel ridges are well elevated along the cephalic margin.

Description. The cranidium is convex, subquadrate in outline, with a broad, flat, concave anterior brim and conical glabella. The glabella is deeply marked by two pairs of glabellar furrows; the first is faint and located posterior of the mid-line of the glabella (tr.), the second pair is deep, directed posterior laterally from the mid-line of the glabella, and terminates before reaching the occipital furrow. The dorsal furrows are deep and broad. The occipital furrow is narrow and steep-sided at the sides of the glabellar base; the crescentic occipital ring is wider than the glabellar base (tr.), and bears a median tubercle. The broad preglabellar field is about one-half as



Text-fig. 53: Phaseolops conus, n. sp. A,B, top and ventral views of anaprotaspides, x 56; C,D, two paraprotaspides, x 53, x 46; E, early meraspis, x 30; F,G, two late meraspides, x 31, x 28; H,I, top and ventral views of two librigena, x 6, x 4; J, holaspid cranidium, x 12; K,L, ventral and dorsal views of two pygidia, x 11, x 10. (Drawings made from photographs.)

long as the glabella (sag.); it is gently convex and ventrally curved; the convex anterior border is broad and of about the same width as the preglabellar field; it is distinctly delimited by the anterior furrow. The convex fixigenae are narrow, about one-fourth as wide as the glabella; the palpebral lobes are medium-sized, semi-circular and broadly flattened; the palpebral furrows distinctly marked between the fixigenae and palpebral lobes. They are acute laterally at the mid-line of the palpebral lobes; the posterior fixigenae are narrow and delimited by marginal furrows; the posterior fixigenal borders are narrow, being about two-thirds as wide as the occipital ring, and are sharply pointed laterally. The anterior branches of the facial sutures are strongly divergently convex, and the posterior branches are divergently straight or slightly sinuous. The underside of the cranidium has a narrow anterior border doublure, and the posterior margin has a broad occipital one. The occipital doublure is broad at the central axis and tapers laterally toward the ends of the posterior fixigenal borders.

The librigena is elongate, with a medium-narrow ocular platform; the lateral and posterior furrows are both shallow but distinctly impressed; they join at the genal angle and extend along the genal spine for a short distance. The underside of the librigena bears a broad lateral doublure, which is sharply pointed anteriorly and curves posterior-laterally to end at the ocular base.

The pygidium is subtriangular and convex; its axial lobe is conical and tapers posteriorly, extending about two-thirds the length of the pygidium (sag.); the axial ring furrows are shallow and undulatory;

the pleural lobes are divided into three pleural bands, which are impressed by pleural furrows and directed laterally and posteriorly into short spines; the posterior axial lobe is a flat, gently convex area, without any pleural or interpleural furrows. The underside of the pygidium has a broad doublure along the posterior margin and is notched post-axially.

The surface of the skeleton is covered by scattered large granules, and bears fine radial caeca at the anterior brim; the outside of the cephalic margin and the doublures bear parallel ridges along the border.

Remarks. This species closely resembles P. sepositus Whittington (1963), the type species, from the Middle Ordovician of Lower Cow Head, western Newfoundland, but it differs in having a cranidium with a broader anterior border, conical glabella, and indistinct glabellar furrows; the associated pygidium has a slightly shorter axial lobe and wider, more distinct fing-furrows.

The present species is represented by more than one hundred immature and mature specimens. All were etched from a few small pieces of black, finely crystalline limestone. The materials include very abundant instars of many different genera, but the present forms are distinguished from others by their gently convex or nearly flat skeletons, and the unornamented surface, (excluding a pair of anterior pits.).

Horizon and Locality. Middle Ordovician, Edinburg Formation. 1.5 mile, Southeastern Strasburg Junction, Virginia.

Figured specimens. Holotype, Cranidium, U.C.M. 38742.

Paratype, Cranidia, U.C.M. 38742p-r.

Librigenae, U.C.M. 38742t-v.

Pygidia, U.C.M. 38742x-z, a'.

Phaseolops conus, n. sp., ontogeny

Anaprotaspid stage (Pl. 17, figs. 1-3 and text-fig. 53A, B). The shield is rounded, flat, gently convex, and about 0.27 mm. in length (sag.). The surface lacks any striking features, except for a slight convexity along the axis; there is no distinct dorsal furrow, axis, or pleural lobe divisions. The anterior margin has two small depressions or pits. The posterior lateral border is prolonged as a pair of short, stout spines. The posterior-lateral border is deeply notched. The underside of the shield has a broad, flat doublure along the posterior margin. The surface is roughly to finely granulose.

The specimens are so small and flattened that they are very easily misidentified as different animals. They were at first thought to be either trilobite hypostomata or ostracods before photographs were taken. However, photographs reveal a pair of pits on the anterior margin and a pair of short spines at the posterior-lateral border which clearly indicate that they are small trilobites.

Paraprotaspid stage (Pl. 17, figs. 4-8,22 and text-fig. 53C, D). The shield is elongate-oval, moderately convex, and varies from 0.40 to 0.55 mm. in length (sag.). The axial and pleural lobes are separated dorsal furrows. The axial lobe is slenderly fusiform, without any distinct axial rings or posterior cephalic border. The pleural lobes are about the same width as the glabella; the palpebral lobes are small and located at one-third the shield length from the anterior end; the

anterior facial sutures are convergent, and the posterior ones are divergently straight and terminate at two-thirds the shield length from the anterior end. The protopygidium is not definitely differentiated from the cephalon, but the facial sutures give the best clue for judging the pygidial position and shape: it is a transversely semi-circular region located behind the posterior branch of the facial sutures; the axial lobe is defined by distinct furrows; the pleural lobes are gently convex, curving ventrally to the margin, without pleural furrows or interpleural grooves. The under side of the shield has a uniformly narrow posterior doublure. The surface is covered by fine granules.

It seems that there is a growth gap between the anaprotaspid and the present stage; this gap is indicated by the fact that the anaprotaspis lacks both protopygidium and facial suture, and the paraprotaspis suddenly shows these well developed. Such an ontogenetic saltation is incompatible with other trilobite development, and it appears that the metaprotaspid stage is missing here. Probably the lack reflects the meager nature of the materials available. In comparing the morphologic features of the anaprotaspis and paraprotaspis one might expect the missing metaprotaspis to be characterized by a rounded to slightly elongate skeleton of low convexity with axial and pleural lobes obscurely differentiated; neither protopygidium or dorsal facial suture are to be expected; the posterior lateral margin of the shield would probably bear a pair of marginal spines.

Early meraspid stage (Pl. 17, figs. 9-12 and text-fig. 53E). The cranidium is subquadrate in outline, convex and about 0.60-0.80 mm. in length (sag.). The glabella is cylindrical but expands slightly

anteriorly; the glabellar furrows are indistinct except for the pre-occipital ring furrow. The occipital ring, which is acute posteriorly, is defined by the occipital furrow and bears a minute median node. The dorsal furrows are well marked, parallel to the sides of the glabella, and slightly expanded laterally at the base of the last pair of glabellar furrows. The anterior border is broad and convex, curves forward, and slightly touches the anterior glabellar margin. The fixigenae are slightly narrower than, or of the same width as, the glabella; the palpebral lobes are sickle-shape, narrow, elongate, and located at the mid-line of the glabella (tr.); the posterior fixigenae are broad, triangular and have their marginal border directed slightly posterior-laterally. The facial suture is slightly divergently convex anteriorly and divergently straight posteriorly. The surface is covered by medium-large granules.

The early meraspid specimens differ from those of the earlier stage in that the cranidium bears distinct anterior and posterior borders, and the palpebral lobes are located more posteriorly.

Late meraspid stage (Pl. 17, figs. 13-16,23,27 and text-fig. 53F, G). The convex cranidium is subquadrate in outline and ranges from 0.90 to 1.20 mm. in length (sag.). The glabella is slenderly conical and marked by two pairs of glabellar furrows; the pre-occipital furrow, or last pair of glabellar furrows, is distinct and convex; the first pair is shallow, short, and located opposite the palpebral lobes. The dorsal furrows are deep and narrow. The occipital ring is crescentic, arches posteriorly, and is defined by a

distinct occipital furrow. The preglabellar field is medium-wide and gently deflected; the convex anterior border is about the same width as the preglabellar field and is distinctly defined by the anterior furrow. The convex fixigenae are about one-half as wide as the glabella, and bear flattened palpebral lobes; the broadly crescentic palpebral lobes are situated at the mid-line of the glabella (tr.), and are distinctly deliminted by palpebral furrows; the posterior fixigenae are narrow, with the marginal border being of the same width as the occipital ring (tr.). The anterior branches of the facial sutures are divergently convex, and the posterior ones are divergently straight. The pygidium is semi-circular or semi-oval and consists of 5 or 6 convex segments, and lacks marginal spines. The pygidium is possibly preceded by 2 or 3 articulating thoracic segments. The surface is covered by large granules, and caeca occur on the preglabellar field.

This stage is distinguished from the previous one by having the cranidium broader and shorter, the fixigenae narrower, and the preglabellar field present. In comparison with holaspid specimens the meraspid ones have broader fixigenae, narrower and more anterior palpebral lobes, and the pygidium is without marginal spines.

Figured specimens. Anaprotaspides, U.C.M. 38742a, b.
Paraprotaspides, U.C.M. 38742c-g.
Early meraspides, U.C.M. 38742h-k.
Late meraspides, U.C.M. 38742lo, s, w.

Family Pterygometopidae Reed, 1905

Genus Calliops Delo, 1935

Calliops strasburgensis Ulrich and Delo

Pl. 18, figs. 1-38 and text-fig. 54.

Calliops strasburgensis Ulrich, E. O., and Delo, D., 1940, p. 99-100, pl. 12, figs. 8-10.

Ptyrygometopus sp. Butts, C., 1941, pl. 82, figs. 9-13.

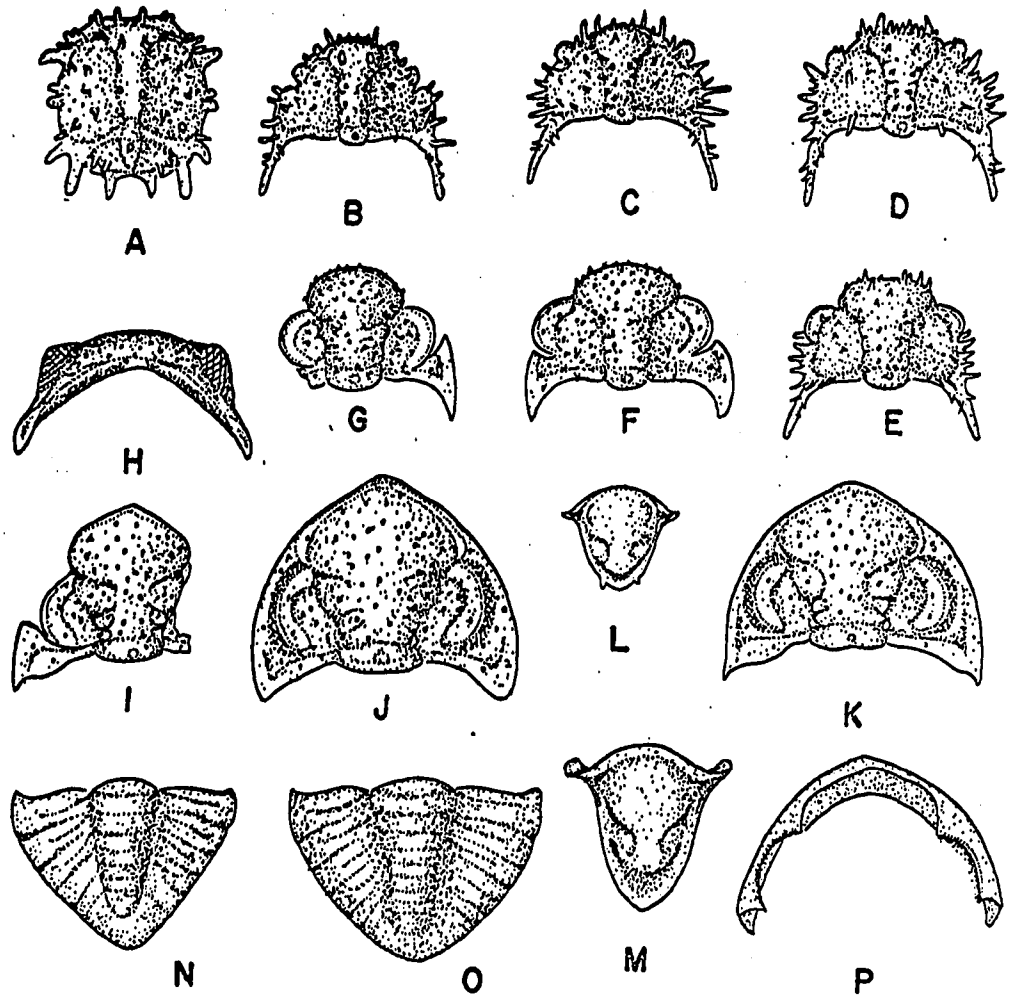
Calliops strasburgensis Ulrich and Delo; Cooper, B., 1953, p. 37, pl. 17, figs. 1-15.

Diagnosis. Cephalon highly convex. Glabella very broadly expanded anteriorly and marked by three pairs of glabellar furrows. Dorsal furrow deep and narrow. Occipital ring broad, convex. No preglabellar field or anterior border. Fixigenae narrow. Palpebral lobe longitudinally sickle-shaped. Rostro-librigenae narrow without median or connective sutures. Hypostoma ovally elongated, with long posterior lateral wings. Thoracic segments convex and stout with rounded, anteriorly directed ends. Pygidium triangular in outline, strongly convex, consisting of more than ten segments. The surface is densely granulose.

Calliops strasburgensis Ulrich and Delo, male?

Pl. 18, figs. 14,15,18,19,26,29,35,38 and text-fig. 54K, O.

Description. The cephalon is semi-circular in outline, highly convex, with a broad cranidium and narrow rostro-librigenae. The glabella is very large and broadly expanded anteriorly; the three pairs of glabellar furrows are deeply marked; the first pair of



Text-fig. 54: Calliops strasburgensis Ulrich and Delo. A, paraprotaspis, x 36; B-E, four early meraspides, x 22, x 34, x 23, x 17; F,G, two late meraspides, x 15, x 10; H, frontal view of a cephalon, x 3.2; I, early holaspis, x 3; J, "female" cephalon, x 3; K, "male" cephalon, x 3.2; L,M, a juvenile and adult hypostoma, x 10, x 3.2; N, "female" pygidium, x 3.8; O, a "male" pygidium, x 3.3; P, a librigeno-rostrum, x 8.7. (Drawings made from photograph.)

glabellar lobes is large and transverse; the second pair is oval and small, the third is pre-occipital and very small. The dorsal furrows are narrow and deeply marked with the anterior ends broadly open. The broad occipital ring is curved slightly anteriorly and bears a tiny median tubercle. There is no anterior border or preglabellar field. The fixigenae are broad; the shallow posterior fixigenal furrows extend anteriorly before reaching the lateral border. A pair of short spines is directed posteriorly from the ends of the rear borders.

The arched rostro-librigenae lack median or connective sutures; the narrow ocular platform slopes steeply down from the ocular ring to the lateral margin; the lateral border is smooth and lacks a lateral furrow.

The hypostoma is elongate, ovate, and moderately convex, with a pair of short, broad lateral wings; the median body is slightly convex, with a pair of elongate lateral maculae; the posterior border is broad, concave and U-shaped; the lateral and posterior margins are narrow and elevated; the anterior border is arched forward and bears a pair of broad, short, tilted wings.

The pygidium is triangular in outline and slightly convex. The convex and conical axial lobe tapers posteriorly with a rounded termination, and is anteriorly divided into four large rings and posteriorly into five or six smaller ones. The border lacks both furrow and spines.

The surface is covered with large granules, except for the hypostoma and pygidium which are finely granulose.

Figured specimens. "male" form. Cranidia, U.C.M. 38743, 38743m, q, w.

Pygidia, U.C.M. 38743d', g'.

Rostro-librigenae, U.C.M. 38743t.

Hypostoma, U.C.M. 38743r.

Calliops strasburgensis Ulrich and Delo, female?

Pl. 18, figs. 16,17,27,32-34,36,37 and text-fig. 54J, N.

Comparison. The presumed female skeletons differ from those of males in that the female cephalon and the glabella are narrower and longer, the anterior cranidial margin is more acute, the rostro-librigenae lack genal spines, and the pygidium has narrower pleural lobes.

Remarks. A few hundred well preserved specimens were etched from several small pieces of black, finely crystalline limestone. The characters of this species conform in general to Urich and Delo's (1940) description, but unfortunately, their material was poorly preserved and reveal inadequate information for reliable comparison. Ulrich and Delo's types were collected from the Edinburg Limestone near Strasburg Junction, Virginia and were refigured by Cooper (1953, p. 37, pl. 17, figs. 6, 13-15). The additional materials were collected from the same general area and formation by Cooper (1953). These are shown in a state of better preservation, and characteristics. The writer's materials are identical with the latter ones. One of Cooper's adult specimens shows at least 11 thoracic segments (his pl. 17, fig. 12).

Horizon and Locality. Middle Ordovician, Chambersburg Limestone, Willow Groove, 3 miles Southwest of Woodstock, Virginia.

Figured specimens. "female" form. Cranidia, U.C.M. 38743o, p. Pygidia, U.C.M. 38743a'-f'.

Calliops strasburgensis Ulrich and Delo, ontogeny

Paraprotaspid stage (Pl. 18, figs. 1,2, and text-fig. 54A). The rounded and convex shield with distinctly separated axial and pleural lobes, is approximately 0.57 mm. in length (sag.). The convex axial lobe is strongly expanded anteriorly, without distinct ring furrows; the frontal lobe is bradly triangular, and well defined by furrows. The convex pleural lobes slope down steeply along the lateral margin; the posterior lateral borders are not clearly recognizable. The transversely subtriangular protopygidium is separated from the cephalon by a faint and anteriorly arching furrow; the axial and pleural lobes lack distinct furrows. The surface is covered by granules and spines. The anterior margin of the frontal lobe is marked by a pair of stout spines on the anterior-lateral corners and a pair of short ones at the center; the posterior lateral corners of the frontal lobe have a pair of vertically directed spines; the axial lobe, exclusive of the frontal lobe and protopygidium, is cylindrical with four pairs of tiny tubercles. The fixigenal surface has four pairs of nodes, of which two pairs are located anterior-laterally, and the other posteriorly; the fixigenal margin bears a pair of large spines behind the palpebral lobes, three short ones laterally and posteriorly, and a larger pair projecting posteriorly. The protopygidium has a spiny margin.

Early meraspid stage (Pl. 18, figs. 3-9 and text-fig. 54B-E). The convex cranidium is about 0.60-0.85 mm. long (sag.) is semi-oval in

outline and has a pair of long, posteriorly directed fixigenal spines. The glabella is distinctly defined by dorsal furrows and divided into four rings by furrows; the frontal lobe is broad and expanded anteriorly; the glabellar furrows are deep laterally but shallow across the central axis; the occipital ring is convex, crescentic and bears a median tubercle; no anterior border or preglabellar field are seen. The fixigenae are broad posteriorly. The palpebral lobes are small and located opposite (tr.) the first glabellar furrow. The outer surface is covered by both fine and coarse granules and spines; the inner surface is finely punctate and spinose.

Late meraspid stage (Pl. 18, figs. 10-13,20,23,24,30-31 and text-fig. 54F, G). The semi-circular cranidium is about 0.90-1.50 mm. in length (sag.). The glabella is broadly expanded anterirorly and has a narrower (sag.) preoccipital segment; the glabellar furrows are distinctly separated and directed posterior-laterally; the large palpebral lobes are convex above the dorsal furrows. The posterior fixigenae are narrow and have a wide lateral protion; the posterior-lateral border bears a pair of short terminal spines, directed backwardly. The librigenae lack median or connective sutures and are arched; the ocular platforms are narrow and almost vertical; the anterior and later borders bear wide spines. The hypostoma is ovate, moderately convex, and with a vertically curved marginal border. A pair of short, delicate spines extends from the posterior-lateral margins. The pygidium is triangular in outline and divided into 6 or 7 segments by distinct furrows; each segment ends in a pair of posterior-laterally directed spines. The surface is coarsely granulose and the

anterior glabella and librigenal borders are spinose.

The main morphologicchanges of this stage are: the supplanting of the spinosity in earlier instars by granulation; the enlargement of the palpebral lobes and their shifting from the anterior fixigenae to the rear portion; the posterior fixigena which was broad in earlier instars now becomes narrower; the fixigenal spines decrease in size; the ocular platform broadens; and the hypostoma loses its spines; the formerly spinosely fringed pygidium now has smooth margins.

Figured specimens. Paraprotaspides, U.C.M. 38743a.
Early meraspides, U.C.M. 38743b-h.
Late meraspides, U.C.M. 38743i-l, s, u, v, y, z.

Family Calymenidae Burmeister, 1843

Genus Flexicalymene Shirley, 1936

Flexicalymene granulosa (Foerste)

Pl. 19, figs. 1-29 and text-fig. 55

Calymene callicephala granulosa Foerste, A. F., 1909, p. 294.

C. granulosa Foerste, Bassler, R. S., 1919, p. 356, pl. 56, figs. 1, 2.

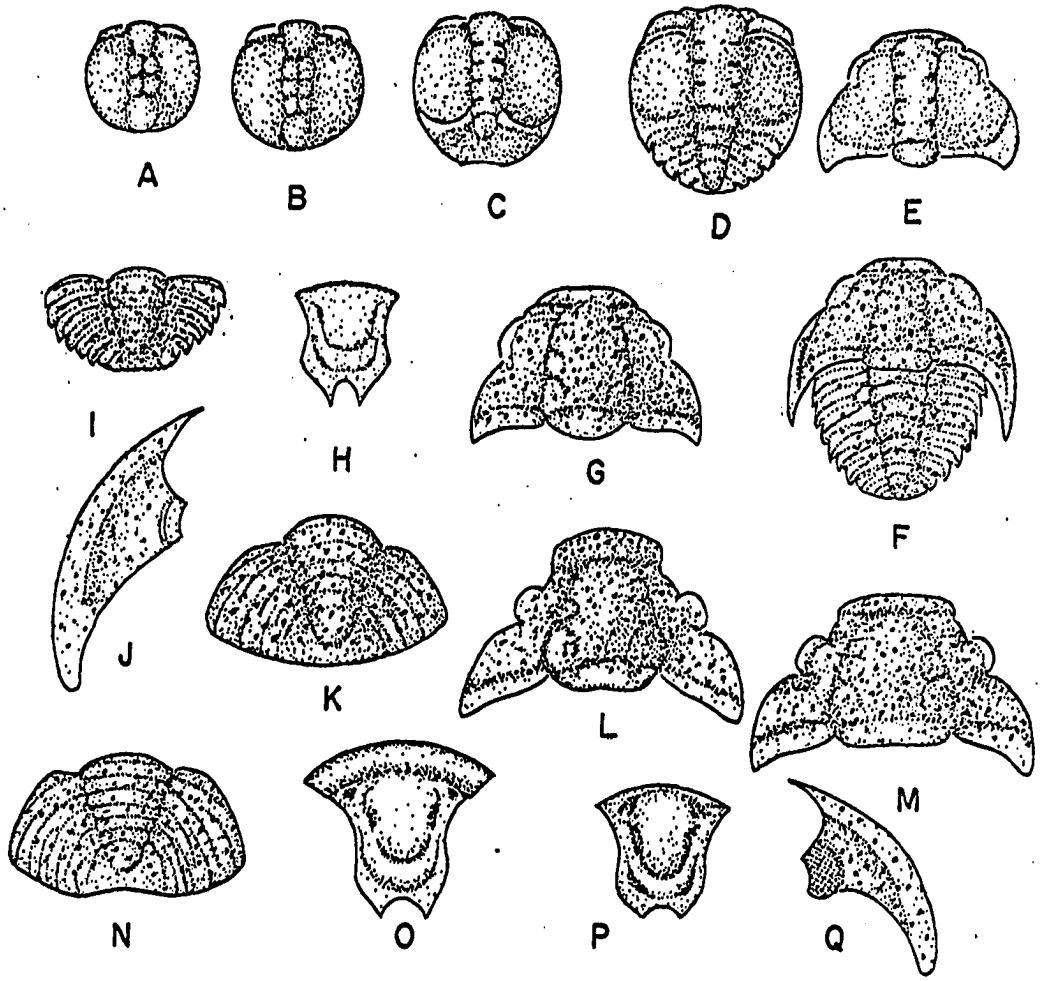
Flexicalymene granulosa (Foerste), Bucher, W. H., Caster, K. E., Jones, S. M., and Dalvé, E., 1939, 1945, and 1961, pl. 2, figs. 9, 10.

Diagnosis. Cranidium trapezoidal in outline and convex. Glabella broadly conical, with three pairs of deeply marked glabellar furrows. Dorsal furrow very deep. Occipital ring convex. No preglabellar field. Anterior border of medium width. Fixigenae narrow anteriorly and broad posteriorly. Palpebral lobes small, located well in front of the mid-length of the glabella. Hypostoma subquadrate and slightly convex, with a pair of posterior marginal spines. Librigenae elongate, with or without genal spines. Thorax divided into 13 segments. Pygidium triangular or subtriangular in outline, convex, with five distinctly marked segments and a small terminal portion. Surface covered with medium coarse granules.

Flexicalymene granulosa (Foerste), male?

Pl. 19, figs. 17,18,19B,22,23,26-28 and text-fig. 55J, K, M.

Description. The cranidium is trapezoidal in outline and convex. The glabella is broadly truncate-conical and convex above the fixigenae; the first pair of glabellar furrows is short and shallow and directed anterior-medially from the dorsal furrow; the second pair is short and



Text-fig. 55: A growth sequence of Flexicalymene granulosa (Foerste). A, anaprotaspis, x 52; B, metaportaspis, x 50; C,D, two paraprotaspides, x 40, x 31; E, early meraspis, x 26; F,G, two late meraspides, x 14, x 13; H, immature hypostoma, x 20; I, small pygidium, x 24; J, "male" librignea, x 2; K, "male" pygidium, x 4.5; L, medium sized "female" cranidium, x 15; M, large sized "male" cranidium, x 4.2; N, "female" pygidium, x 14; O, medium sized hypostoma, associated with rostrum, x 14; P, adult hypostoma, x 6; Q, "female" librignea, x 13. (Drawings made from photographs; except for B, schematic.)

deeply depressed with distinct pits; the third pair of furrows is longer, deeper, and directed slightly posteriorly with bifurcations at the ends. The glabellar lobes are rounded elongate and increase in size from the anterior to the posterior pair. The dorsal furrow is deep and broad, and curves inward behind the last pair of glabellar lobes. The occipital furrow is deep laterally but shallow and swings forward at the axial line. The anterior brim lacks a preglabellar field; the anterior furrow is deep and straight; the anterior border is narrow, convex and arches slightly anteriorly. The subtriangular fixigenae slope anteriorly and laterally downward from the palpebral lobes, which are located between the first and second glabellar furrows (tr.). The anterior facial suture is convergent, and the posterior one is divergently convex. The posterior fixigenal furrow is shallow and broad; the marginal borders are convex and about the same width as the occipital ring (tr.).

The librigena is elongate with a short and stout genal spine; the ocular platform is moderately broad, convex, and has a small ocular ring; the lateral border is roundly convex and delimited by a shallow broad, lateral furrow.

The hypostoma is subquadrate in outline; its median body is gently convex; the posterior lobe is U-shaped, gently convex, and delimited by furrows. The marginal border is convex laterally and flattened posteriorly with a pair of posteriorly directed spines. The lateral furrow is deep and occupied by two pairs of elongate pits. The anterior lateral wings are concave, broad, and triangular, and have a pair of rounded and rather deeply marked pits.

The rostral plate is gently convex, narrow, and transverse and curves slightly forward. The thorax is divided into 13 segments. The axial rings are strongly convex and associated with deeply marked furrows. The pleural lobes are narrower than the axis, gently convex, and curve ventrally. The ends of each pleural segment are rounded without spines.

The pygidium is subtriangular in outline and strongly convex. The conical lobe tapers posteriorly and is divided by distinct ring furrows into 4 or 5 rings and a triangular terminal portion. The dorsal furrow is well impressed; the terminal portion which is set off by distinct ring furrows, end before reaching the posterior margin. The pleural lobes gently curve ventrally and are separated into 4 or 5 pleural lobes by narrow interpleural grooves. No marginal border or marginal spines are present.

The surface of the skeleton is covered by fine to medium sized granules.

Figured specimens. "male" form. Cranidia, U.C.M. 38744q-s.
Pygidia, U.C.M. 38744v, w.
Librigena, U.C.M. 38744b'.
Hypostomata, U.C.M. 38744z, a'.

Flexicalymene granulosa (Foerste), female?

Pl. 19, figs. 15,19A,24,29, and text-fig. 55L, N. Q.

Comparison. The "female" forms differ from the "male" in that the cranidium has a broader anterior furrow, broader anterior border, and more posteriorly located palpebral lobes. The librigenae have

narrower ocular platforms and lack genal spines. The pygidium is quadrate or subrounded in outline.

Remarks. According to Bassler (1919) and Dalvé (1948), two species of Flexicalymene are found in the Cincinnati area, i.e., F. granulosa and F. meeki. F. granulosa, which occurs in the Eden Formation, the lower part of the Cincinnatian, is characterized by a smaller skeleton and granulose surface. F. meeki which occurs in the Maysville and Richmond Formations, the Upper Cincinnatian, is characterized by a larger-sized skeleton and more finely granulose surface (pl. 19, figs. 30-32). The materials here studied were collected from the Eden Shale. The material contains three other trilobite genera: Isotelus, Cryptolithus, and Primaspis.

About 80 specimens, both immature and mature forms, were prepared from 50 kg. of grey to yellowish-brown shale; the small instars are very rare and adult fragments common; most of the specimens are slightly deformed. The "female" form here reported has not been found beofre, and while it may belong to a new species, and certainly would have been so designated in accord with previous taxonomic procedure, here is interpreted as a sexual difference within F. granulosa, comparable dimorphism occurs in other materials herein reported. The sexual ratio is about 385.

Horizon and Locality. Upper Ordovician, Cincinnatian, Eden Formation, Park Hills, western Covington, west side of Highway Route 42, Kentucky.

Figured specimens. "female form". Cranidia, U.C.M. 38733o, s.
Pygidium, U.C.M. 38744x.

Librigena, U.C.M. 38744c'.

Flexicalymene granulose (Foerste), ontogeny

Anaprotaspid stage (Pl. 19, figs. 1-4 and text-fig. 55A). The rounded to moderately convex shield with the axial and pleural lobes distinctly separated, ranges from 0.24 to 0.28 mm. in length (sag.). The axial lobe consists of an elongate frontal lobe, two pairs of central nodes, and a large, convex terminal one. The dorsal furrows are distinct; an axial fissure extends from behind the frontal lobe to the front of the terminal tubercle. The supercilioid ridges are broadly convex, and distinctly separated from the pleural lobes by furrows. The convex pleural lobes are broadly convex, and distinctly separated from the pleural lobes by furrows. The convex pleural lobes are about one and one-half times wider than the axis. The surface is finely granulose.

Metaprotaspid stage (Text-fig. 55B). The moderately convex shield is spherical to subspherical in outline, and approximately 0.35 mm. in length (sag.). The conical axial lobe tapers slightly posteriorly and is divided into 5 rings with a well defined central axial fissure; the frontal lobe is rounded with a pair of narrow supercilioid ridges extending laterally; the second, third and fourth ones are transverse and of about the same size. The dorsal furrow is distinct. The palpebral lobes are convex and about twice the width of the glabella. A broad unsegmented area is located behind the fith axial ring. A longitudinal fissure extends along the central axis. The surface is covered by granules.

No metaprotaspid specimens have been recovered, but the morphologic differences between the anaprotaspis early forms, with four axial rings, and the early meraspis, with more than six axial rings, clearly indicate that the stage with five axial rings is lacking. The absence of the metaprotaspid instar in F. granulose may be due to preservation, meagerness of materials, or ecologic adaptation of planktonic larvae. In any case, the early immature specimens of the present material are very rare.

Paraprotaspid stage (Pl. 19, figs. 5-10 and text-fig. 55C, D). The moderately convex, subrounded shield is composed of a protopygidium and cephalon with distinct glabella and fixigenae; it varies from 0.45 to 0.70 mm. in length (sag.). The glabella is cylindrical to slightly expanded anteriorly; it is divided into four rings; the glabellar furrows are deep laterally, shallow across the axis, and straight or slightly curved posteriorly; the transverse occipital ring is delimited by the occipital furrow. The prominent eye-brow-like ridges extend posterior-laterally from the frontal lobe or first glabellar ring. The convex fixigenae slope down toward the lateral margin and are approximately one and one-half times wider than the glabella. The rear fixigenal borders extend posterior-laterally and are faintly delimited by a marginal furrow. The semi-circular to subtriangular protopygidium is formed of 2 or 4 segments. The conical axial lobe tapers posteriorly with impressed ring furrows. The pleural furrows and the interpleural grooves are distinctly defined. The surface is covered by granules.

This stage differs from the previous one in having the distinct

protopygidium, and the posterior fixigenae expanded laterally.

Early mersapid stage (Pl. 19, figs. 11-12, 20 and text-fig. 55E). The cranidium which is about 0.70-0.85 mm. in length (sag.), and is convex and trapezoidal in outline. The glabella is cylindrical and has three pairs of minute glabellar furrows. The dorsal furrows are deep and parallel. The occipital ring is crescentic, and has a tiny median node. The fixigenae are narrow between the palpebral lobes but broad and convex posteriorly; the posterior border which are directed posterior laterally before terminating laterally, are defined by marginal furrows and are approximately twice as wide as the occipital ring (tr.); the small palpebral lobes are situated at one-fourth the length of the glabella from the anterior margin. A narrow preglabellar brim arches anteriorly along the anterior margin of the glabella. The transverse oval pygidium is preceded by three articulating thoracic segments; its convex axial lobe is conical, tapers posteriorly, and is divided by ring furrows; the pleural lobes are the same width as the axis and deeply marked by three pairs of interpleural grooves. The posterior margin bears short spines. The surface of the skeleton is covered by granules.

The important characters of this stage are that the glabella is cylindrical, the eye-ridges are distinct, and the preglabellar brim first appear.

Late meraspid stage (Pl. 20, figs. 13,14,16,21,25 and text-fig. 55F, G). The cranidium is about 0.8-0.14 mm. long (sag.). The conical glabella is deeply marked by three pairs of glabellar furrows; the dorsal furrow is deep and broad; the occipital ring has a tiny median

tubercle. The anterior border is separated by a deeply impressed anterior furrow. The fixigenae are about one-half as wide as the glabella between the palpebral lobes and the dorsal furrows; the posterior fixigenae are broad with the posterior border projecting posteriorly before terminating. The hypostoma is subquadrate, gently convex and has a pair of spines projecting posteriorly. The semi-circular pygidium is divided into 5 or 6 segments, and each segment is directed slightly posterior-laterally from the convex axis and ends in a pair of spines.

The surface of the skeleton is covered by both fine and coarse granules.

Figured specimens. Anaprotaspides, U.C.M. 38744a-d.
Paraprotaspides, U.C.M. 38744e-j.
Early meraspides, U.C.M. 38744k, l, t.
Late meraspides, U.C.M. 38744m, n, p, u, y.

Family Trinucleidae Hawle and Corda, 1847

Genus Cryptolithus Green, 1838

Cryptolithus bellulus (Ulrich)

Pl. 20, figs. 1-13 and text-fig. 56.

Trinucleus bellulus Ulrich, E. O., 1878, p. 99-100, pl. 4, fig. 15.

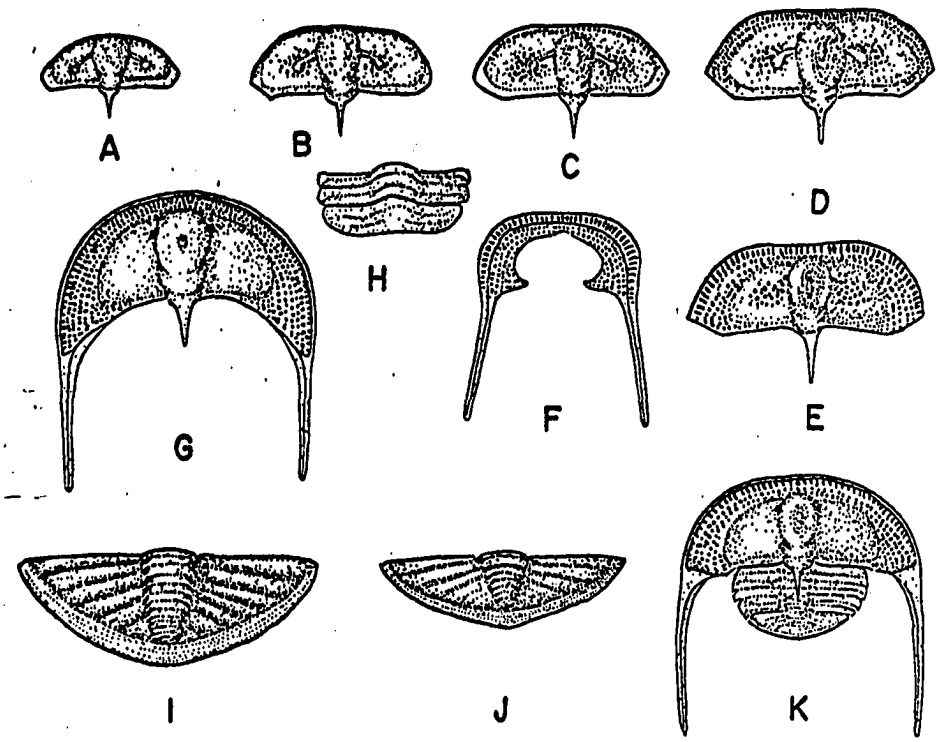
Cryptolithus recurus (Ulrich), Bassler, R. S., 1919, p. 334-335, pl. 56, figs. 14-17.

Cryptolithus lorrainensis Ruedemann, R., 1926, p. 107-115, pl. 21, figs. 4-5.

Cryptolithus bellulus (Ulrich), Whittington, H. B., 1941a, p. 30-34, pl. 5, figs. 1,7-9,13,14,19,21,22,25,26,28.

Diagnosis. Cephalon semi-circular in outline and moderately convex, with a broad pitted fringe. Glabella ovate and convex above the fixigenae. Occipital ring bearing a long, stout median spine. Thorax divided into six thoracic segments with convex axial rings and flat pleural lobes. Pygidium sub-triangular in outline, with slightly elevated axial lobe and flattened pleural lobes. Ridged marginal border elevated and convex, but curved ventrally.

Description. The skeleton is rounded to subrounded in outline and has a rather large cephalon and a small pygidium. The cranidium is semi-circular in outline and extends about one-half the body length. The glabella is ovate, elongate, and convex, above the fixigenae; the glabellar furrows are deep laterally, the posterior ones being deeper than the anterior ones; a median tubercle occurs at one-third the length of the glabella from the anterior. The dorsal furrow is shallow and broad. The occipital ring is narrow, curves backward, and is drawn



Text-fig. 56: Cryptolithus bellulus (Ulrich). A, paraprotaspis, x 23; B,C,D, three early meraspides, x 20, x 19, x 8; E, late meraspis, x 3.4; F, ventral view of lower lamella, x 2.5; G, holaspid cephalon, x 1.8; H, early meraspid pygidium associated with two thoracic segments, x 18; I,J, meraspis, x 5. (Drawings from photographs.)

out into a stout occipital spine. The fixigenae measured from the inner margin of the fringe to the dorsal furrow at the mid-line of the glabella, are approximately one and one-half times wider than the glabella. The posterior lateral fixigenae have deep and laterally widened marginal furrows; the posterior fixigenal borders are curved slightly backward before reaching the lateral ends. The fringe slopes downward, widens laterally, and narrows in front of the glabella; it is marked by concentric rows of pits; the outer margin of the fringe bears two essentially concentric rows of pits; the outer ones are elongate; the inner ones are all rounded and smaller; a few additional pits occur posterior-laterally at the rear fixigenal border, where the concentric arrangement of pits is lost. The lower lamella or rostro-librigena is broad and of the same shape as the region of the fringe, except for a pair of genal spines directed posteriorly; the inner surface of the lamella bears shallow tubercles, the arrangement of the tubercles is the same as of the pits on the upper lamella or cranidium; the under surface of the lamella shows pits (pl. 20, fig. 7) the shape and arrangement of which conforms to those of the cranidial frings; a prominent ridge or girder occurs along the anterior cranidial margin; between the first and second rows of pits which extends continuously into the genal spines.

The thorax is divided into six segments; the axial lobe is convex above the pleural lobes; the dorsal furrow is shallow and marked with a pair of distinct pits on each segment. The pleural segments are flat and directed laterally, with a pair of short terminal spines projecting posteriorly. The pleural furrows are shallow and wide.

The pygidium is transversely subtriangular in outline; the axial lobe is convex, slightly elevated above the pleural lobe, and divided into more than ten axial rings; the first and second ring furrows are distinct, and the following are faint or almost indistinguishable; the pleural lobes are flat, separated by four pairs of ridges anteriorly, and indistinctly separated posteriorly. The broad and prominent margin has a ridge rising from the inner marginal border; the outer margin slopes steeply downward and is marked with fine, parallel, well elevated ridges.

Remarks. More than one hundred specimens were prepared from 50 kg. of yellowish-brown shale, and include immature and mature forms, both of which are moderately common, but most of the specimens are slightly deformed.

According to Bassler (1915, p. 1471) and Dalvé (1948), two species occur in the Eden Shale of the Cincinnati area, i.e., C. tesselatus and C. bellulus. The specific assignment of the present material is in accord with Whittington's (1941) criteria.

It is interesting to note that the small instars of the present species have well developed eye-tubercles, which have gradually disappeared in the larger instars. It is evident that the mode of life changed during the ontogenetic development of the animal; the early larvae were apparently planktonic, whereas the mature stage was benthonic. The ontogeny suggests that the ancestor of the present species may very well have possessed eyes. This suggests original existance in a photic environment from which the trilobite migrated into the dark or subsurface during which they were progressively reduced,

just as in certain cave fish, polychaetes, etc. with similar life history. The animal (C. bellulus) was possibly a burrower in the substrata, a nocturnal animal, or, perchance, lived below light penetration on the sea-floor.

It is also noteworthy that most of the immature specimens have the upper and lower lamellae of the rostro-librigena preserved separately, whereas those of adults are fused without separation; this phenomenon suggests that possibly the suture which lies between the lamella and the cranidium facilitated ecdysis during early stages, but ecdysis took other paths in the adult stage. This feature has also been observed in Calliops strasburgensis (pl. 18, figs. 1-15 and 16-19) and also is the situation in modern Xiphosura (p. 57).

Horizon and Locality. Upper Ordovician, Cincinnatian, Eden Shale Formation, Park Hills, western Covington, west side of Highway Route 42, Kentucky.

Figured specimens. Cephalon, U.C.M. 38745.
Pygidia, U.C.M. 38745j, k.

Cryptolitnus bellulus (Ulrich), ontogeny

Paraprotaspid stage (Pl. 20, fig. 1, and text-fig. 56A). The cranidium is transverse, semi-circular in outline, moderately convex, and about 0.35 mm. long (sag.). The glabella is elongate, oval, and expanded anteriorly; no glabellar furrows are observed except for a pair of elongate pits on the sides of the posterior portion; the narrow occipital ring is defined by the occipital furrow. No preglabellar field or anterior borders are seen. The fixigenae are triangular and

gently convex with a rounded margin; the prominent eye-ridges curve posterior-laterally from the distal lateral sides of the glabella, and end at a pair of eye tubercles without reaching the rear fixigenal border. The later is prominent and turned slightly anterior-laterally. The surface is finely granulose.

Early meraspid stage (Pl. 20, figs. 2-5, 10 and text-fig. 56B-D). The moderately convex cranidium is semi-circular in outline, and ranges from 0.45 to 1.00 mm. in length (sag.). The glabella is elongate, convex above the fixigenae, and distinctly defined by a pair of posterior glabellar furrows. The dorsal furrow is bradly impressed, has a pair of eye ridges directed posterior laterally, and ends with a pair of eye tubercles on the center of the fixigenae. The anterior border and pitted fringe have appeared. The occipital ring curves posteriorly with a large, posteriorly directed spine. The surface is marked with fine punctae surrounding the eye tubercles.

The pygidium is transversely reniform, and consists of two or three segments which are preceded by the same number of articulated thoracic segments. The axial and pleural furrows are deep and clearly defined; the marginal border is upturned.

Late meraspid stage (Pl. 20, figs. 6-8,11 and text-fig. 56E). The cranidium varies from 1.50-3.30 mm. in length (sag.). The glabella is convex; its high-point is located anteriorly and bears a median tubercle. The occipital ring curves backwardly and bears a long posteriorly directed spine. The posterior fixigenal border turns anterior-laterally before terminating. The surface is finely granulated, except for the fringe; scattered punctae surround the eye tubercle area

and the median tubercle of the glabella, but eye tubercles are absent. Five pairs of distinct pits are present on the dorsal furrow of the thorax.

Figured specimens. Paraprotaspis, U.C.M. 38745a.

Early meraspides, U.C.M. 38745b-e, h.

Late meraspides, U.C.M. 38745f-g, i-j.

Family Asaphidae Burmeister, 1843

Genus Isotelus Dekay, 1824

Isotelus stegops Green

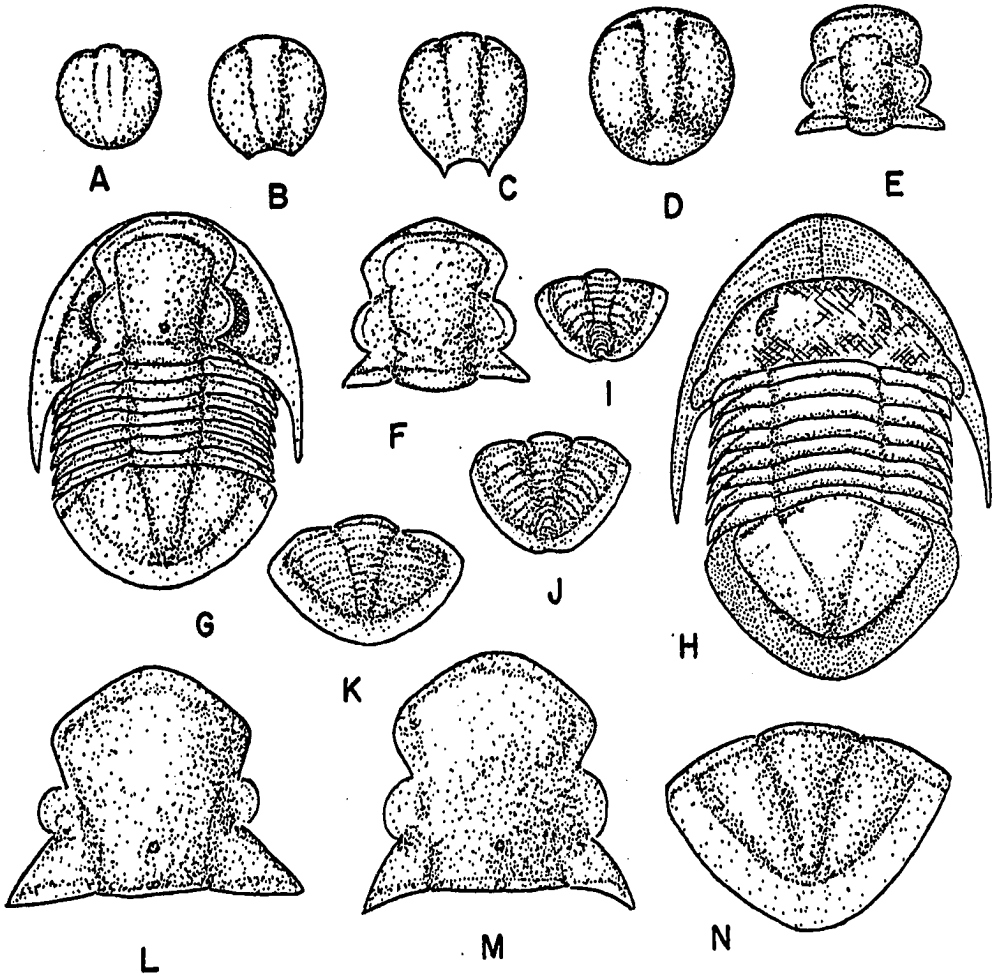
Pl. 20, figs. 14-31 and text-fig. 57.

Isotelus stegops Green, J., 1832, p. 71, casts 26, 27. Bassler, R. S., 1919, p. 342, pl. 56, figs. 3, 4.

Homotelus stegops (Green) Ruedemann, R., 1926, p. 126, pl. 20, fig. 4, pl. 22, fig. 1-9.

Diagnosis. The body is elongate-oval, moderately convex, with poorly defined furrow; both cephalon and pygidium are large; and thorax divided into eight segments. Cranidium flat to gently convex, without distinct glabella, anterior brim or anterior, or posterior borders. Palpebral lobe medium-sized, situated behind mid-length of cranidium. Librigena having medium-sized genal spine. Hypostoma almost parallel-sided; posterior margin with broad, deep notch. Thoracic segments with broader axial ring and shorter pleural lobes. Pygidium roundly triangular, with poorly impressed dorsal and pleural lobe furrows; with flat, broad border. Both cephalon and pygidium with broad marginal doublures.

Description. The cephalon is semi-circular in outline, moderately convex, with broad, flat margins. The cranidium bears a convex axial lobe, is subquadrate in outline and slopes gently downward into a flat anterior brim. The narrow (sag.) occipital ring is defined by a pair of distinct lateral pits, which suggest the posterior ends of the glabella. The palpebral lobes are medium-sized and located behind the mid-line of the cranidium (tr.). The anterior branches of the



Text-fig. 57: Isotelus stegops Green. A, anaprotaspis, x 57; B,C, two metaprotaspides, x 30, x 27; D, paraprotaspis, x 12; E, late early meraspis, x 13; F,G, two late meraspides, x 12, x 3.4; H, ventral view of a complete skeleton, x 1.7; I-K, growth series of pygidia, x 15, x 10, x 4; L, "male" cranidium, x 1.5; M, "female" cranidium. (Drawings made from photographs.)

facial suture are divergently convex and meet at the anterior margin of the cranidium; the posterior branches are divergently straight.

The convex librigenae bear ocular platforms which are broad posteriorly; the lateral borders are broad and concave, but narrower and sharply pointed anteriorly; the genal spines are moderately short; the doublures are flat and broad anteriorly and meet in front of the cranidium at a median suture.

The hypostoma is flat, subquadrate in outline, with a deep posterior notch; no median body or marginal border are present. The lateral wings are broad and short.

The thoracis axis is unusually broad, being twice as wide as the pleural lobes; eight segments are present in the adult form. The dorsal furrows are shallow and broad. The pleural lobes slope gently downward and are directed posteriorly and laterally; pleural lobe furrows are shallowly impressed.

The pygidium is roundly triangular in outline, moderately convex, with a broad, flat marginal border; the axial lobe is slenderly conical, tapering posteriorly and ending at the inner marginal furrow. The axial ring and the pleural segments are not distinctly defined, but at least ten segments are estimated. The doublure is broad, convex, and expands slightly toward the front.

The surface is smooth or covered by punctae, except for a median tubercle on the posterior cranidium; parallel ridges are present along the doublures and the hypostoma. A pair of distinct, rounded pits is impressed on the central portion of the hypostoma.

Remarks. Many beautiful Ordovician specimens have been collected

from the greater Cincinnati area (southeastern Indiana, northern Kentucky, and southwestern Ohio) by students and by amateur paleontologists. Several local collectors have hundreds of Isotelus, Flexicalymene, Cryptolithus, Acidaspis, Isorophus, and Glyptocrinus, etc.. Such abundance is truly remarkable. However, materials here studied are from the writer's collection. While they are less complete than much of the material in amateur hands, they serve admirably to illustrate morphology. According to literature search, about eight species of Isotelus have been published from the greater Cincinnati region:

Isotelus maximus Locke, 1838; Liberty formation, Richmond group, from Treber's Run, Adams County, Ohio.

I. brachycephalus Foerste, 1921; Base of Liberty on top of Waynesville, Richmond group, from Dayton, Oregonia, Warren County, Ohio.

I. megistos Locke, 1842, Upper Maysville Formation, from Adams County, and Cincinnati hill, Ohio.

I. gigas Dekay, in Green, 1832; Yellow argillaceous slate [upper Eden or lower Maysville Formation?], from near Cincinnati, Ohio.

I. stegops Green, 1832; Clay slate [Eden formation?], from near Newport, Kentucky.

I. planus Dekay, in Green, 1832; Yellow argillaceous slate Eden Formation? , from near Newport, Kentucky.

I. covingtonenesis Ulrich, 1914; Cynthiana Formation, from 59.7

and 59.1 miles of Ludlow, near Rogers Gap, North of Cynthiana Station, Kentucky.

Isotelus benjamini Ulrich, 1914; Cynthiana Formation, at 54.5 miles from Ludlow, Sadieville, Rogers Gap, north of Cynthiana Station, Kentucky.

Bassler's (1915) survey of the literature on Isotelus listed three species as occurring in the Ordovician of the Cincinnati area: Isotelus gigas Dekay, I. maximus Locke (both from Maysville Formation), and I. gigas Dekay, I. megistos Locke (both from Richmond). Dalvé (1948) listed only two species: I. gigas and I. maximus. Cumings (1907) said that the common species in the Cincinnati region possesses the genal spine and should be referred to I. maximus Locke and that those fragments which do not show this critical part are indeterminable. Hall, 1847, considered I. gigas, I. planus, and I. stegops to be synonymous. Ruedemann (1926) has placed I. stegops in the genus Homotelus without giving any reasons. It is assumed that Ruedemann's figures are showing the animal as possessing a broader posterior fixigena, forwardly located palpebral lobes, and a rounder pygidium as that of Hemotelus. It is still doubtful that these are any specific or even the generic significance since the sexual dimorphism might exist in the present genus: Isotelus (see below). Foerste (1921) suggested that the two forms occurring in the Richmond strata might represent sexual differences of one species: i.e., I. maxium Locke, about 17-21 inches long, with an elongate cephalon, no librigenal spine, and an elongate-triangular pygidium, is the male form, and I. brachycephalus Foerste, 14.5 inches long with librigenal spine, and with cephalon and pygidium remarkably

shorter and wider, the female. Ross (1967) studied Ordovician trilobites from the Kentucky and Ohio regions, and assigned the Middle Ordovician Isotelus to I. gigas.

As listed above, there are about eight species of Isotelus which have been established around the greater Cincinnati area, ranging in age from Middle to Upper Ordovician (Cynthiana through Cincinnatian). It is difficult to judge the validity of these species, since the characteristics noted are quite ambiguous, and almost none of the criteria employed can serve for species differentiation. Through the Ordovician range noted, the body length increases from 3 or 4 inches in the Cynthiana to 21 inches in the Upper Cincinnatian. Furthermore, if the sexual dimorphism existed here, as suggested by Foerste, it would be exceedingly difficult to separate species based on such criteria as length or width of cranidium and pygidium, genal spine, facial suture, or palpebral lobe position, etc.. Furthermore, both preservation and ontogenetic stage enter into the evaluation of the published "species".

One very interesting observation is evident in the foregoing list of species occurring in the Middle-Upper Ordovician of the Cincinnati area: two "species" have been recognized for each horizon. To what extent, if at all, these reflect sexual dimorphism awaits further study.

Very careful stratigraphic collecting and statistical analysis are imperative if the true nature of Isotelus speciation and variation in the Middle-Upper Ordovician of the classic Cincinnati Ordovician are to be resolved. Unfortunately most amateur collected materials, and this includes much of Museum collections, lacks stratigraphic precision, and

routine professional collecting commonly is not very rewarding. Hundreds of amateurs, seeking trilobites almost to the exclusion of all other fossils, create a quite erroneous impression as to trilobite, and expecially Isotelus, abundance in these local strata. Moreover, most outcrops are stripped of trilobites before the professional collects.

The material of this report was collected from the upper part of the Eden Formation, probably from the lower part of the McMicken member. Therefore, judging from both the stratigraphic position and the morphologic (mainly dimensional) features, I have assigned the materials to I. stegops. The specimens show dimorphism such as Foerste indicated; one group of specimens has elongate cranidia and pygidia, and another group short and broad cranidia and pygidia. It is suggested that the broad and short forms (pl. 20, fig. 30) are male and that the elongate ones (pl. 20, fig. 25, 29) female. Bassler (1919, p.343) has said that what are judged as possible females lack genal spines and the males have them. This interpretation would be in keeping with sexual differences in modern arthropods. (see p. 23).

Horizon and Locality. Upper Ordovician, Cincinnatian, Eden Formation. Park Hills, western Covington, west side of Highway Route 42, Kentucky.

Figured specimens. Cranidium ("mal"), U.C.M. 38746m.
Cranidium ("female"), U.C.M. 38746i, e.
Librigena, U.C.M. 38746n.
Complete skeleton, U.C.M. 38746.

Hypostoma, U.C.M. 38746j.

Isotelus stegops Green, ontogeny

Anaprotaspid stage (Pl. 20, figs. 17, and text-fig. 57A). The shield is rounded, convex and about 0.30 mm. in length (sag); no distinct features occur on the surface except a pair of frontal pits which are present on the anterior margin and suggest the frontal lobe and the orientation of the shield. The surface is covered by rather fine granules.

Metaprotaspid stage (Pl. 20, figs. 18, 19 and text-fig. 57B, C). The shield is subspherical, convex, and about 0.40-0.60 mm. in length. The slenderly fusiform axis is defined by distinct dorsal furrows; no axial rings are seen. The anterior pits are distinctly impressed. The fixigenae are more than one and one-half times wider than the axial lobe. A pair of short, broad spines is directed posteriorly from the posterior lateral margin. The surface is rather finely granulated.

This stage differs from the early one in having the shield distinctly divided into axial and pleural lobes.

Paraprotaspid stage (Pl. 20, figs. 20,21 and text-fig. 57D). The cranidium is elongate, oval in outline, moderately convex and ranges from 0.70 to 1.00 mm. in length (sag.). The glabella is hemi-cylindrical with a pair of distinctive anterior pits on the anterior margin; the glabellar furrows are indistinct and the dorsal furrows are shallow; the occipital ring and the posterior fixigenal border are not differentiated. There is no preglabellar field; the anterior margin is

roundly convex and arches anteriorly. The convex fixigenae are more than one and one-half times wider than the glabella and lack palpebral lobes and ridges.

Late aspect of the early meraspid stage (Pl. 20, figs. 14,15,22, and text-fig. 57E, I, J). The cranidium is subquadrate in outline, about 1.30-1.45 mm. in length (sag.), with broad palpebral lobe located behind the mid-line of the glabella (tr.). The glabella is broadly himi-cylindrical and marked by three pairs of glabellar furrows. The preglabellar field and anterior border have both appeared.

The pygidium is roundly triangular and convex. The axial lobe is conical, tapers posteriorly and ends with a broad, triangular terminal portion. The axis is divided into six rings by well-defined-ring-furrows; the terminal portion consists of three concentric wrinkles and a ridge directed posteriorly to the marginal border. The pleural lobes are marked by six pleural furrows, and the same number of interpleural grooves. At least one thoracic segment is associated with the pygidium. The surface is covered by fine granules.

The characteristics of this stage are quite different from the paraprotaspis, but closely similar to the late meraspis. Hence the specimens of this ontogenetic stage seen here adjudged as belonging to a later aspect of the early meraspid stage; considerable record between this and the paraprotaspis seems to be lacking. The gap is quite possibly due to the meager nature of the collections.

Late meraspid stage (Pl. 20, figs. 23,24,27 and text-fig. 57F, G, K). The cranidium is subquadrate in outline, moderately convex, with distinctly impressed dorsal furrows, and ranges from 1.50 to 2.00 mm.

in length (sag.). The glabella is hemi-cylindrical to strongly expanded anteriorly with three pairs of moderately impressed glabellar furrows. The occipital ring is convex and slightly expanded at the axial line. The anterior furrow is convex, and broader at the median notch; no preglabellar field is present, except in smaller specimens which show a narrow, flat area in front of the glabella; the anterior border is subtriangular, narrow, and anteriorly projecting. The fixigenae are narrower than in the previous stage, being one-half or less than one-half as wide as the glabella; they are flat to gently upturned; the palpebral lobe is medium-sized and located somewhat posterior to the mid-line of the glabella (tr.). The posterior-lateral fixigenae are narrowly triangular, being about one-third as wide as the occipital ring.

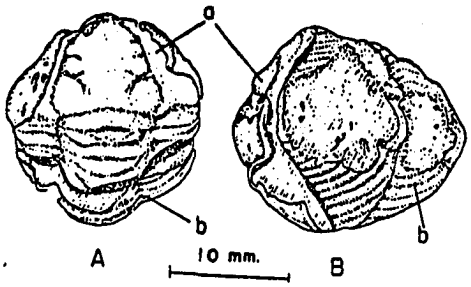
The pygidium is subtriangular, convex, without distinct axial or pleural furrows; fine, parallel ridges are marked along the pleural bands on the inner skeletal surface.

Figures specimens. Anaprotaspis, U.C.M. 38746a.
Metaprotaspides, U.C.M. 38746b, c.
Parprotaspides, U.C.M. 38746d, e.
Late-Early meraspides, U.C.M. 38746o, p, f.
Late meraspides, U.C.M. 38746g, h, k.

Dimorphic Trilobite Problematica

Endo (1937) reported a specimen from the southern Manchuria, Middle Cambrian, which shows two well-preserved trilobites, Fentienia peculiaria Endo, lying side by side joined at the tip of the pygidium as though they are in copulation. The left individual is larger than the right one, and has a larger pygidium. The larger body may belong to the female and the smaller one to the male. If this association is rightly interpreted, it is the first example of copulation yet reported from the Trilobita, and serves admirably to to account for the new widely documented dimorphism in trilobite assemblages of closely similar morphology. Two similar specimens of Flexicalymene meeki (Foerste) and Acidaspis cincinnatiensis Meek in the Geology Museum at the University of Cincinnati seem to document the same act and dimorphism. Both are from older collections carrying the general label from the "Upper Cincinnatian, Cincinnati area". The following is a brief discussion of two specimens.

1. Flexicalymene meeki (Foerste) (pl. 19, fig. 30-32 and text-fig. 58A, B). The two individuals are rolled into cone-in-cone form, cephalon directed to cephalon, and pygidium to pygidium. The two dorsa curve outwardly. The specimen is ovoid, about 19.6 mm. in maximum, and 12.2 mm. in minimum diameters. Both of the individuals have their pygidia slightly weathered and the outer individual (text-fig. 58"b") has the cephalon broken off. Hence the close morphologic comparisons that are desirable are impossible, however, the inner, or "a" form, has the relatively larger pygidium.

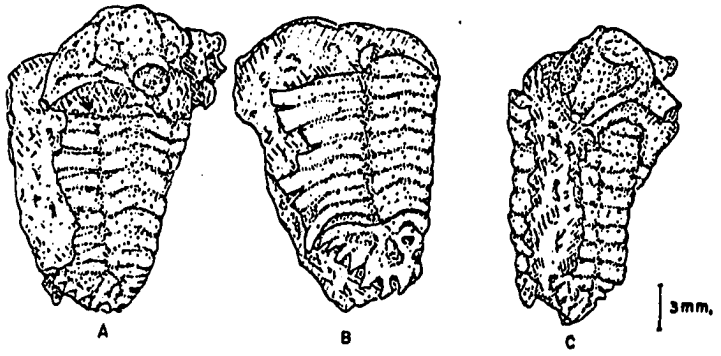


Text-fig. 58: Flexicalymene meeki (Foerste). Showing two individuals lying in a "cone-in-cone" relationship; A, dorsal view; B, ventral view; "a" individual lying in "b". (Drawings made from a photograph.)

There are three possible causes for the enrolled preservation of the animals: a) skeletal moulting, b) accidental preservation, and c) sexual conjugation.

Exoskeletal moulting is common to most crustaceans, xiphosurans, insects, etc.. During their ecdysial period the animals are quite inactive, and their new skeletons are soft and thin. This condition seems hardly to apply to this specimen, since the soft body of newly molted animal is hardly preserved as a fossil. Moreover, the specimen shows both individuals have skeletons of the same thickness, and both are apparently well calcified. The cause of possible accidental preservation may be interpreted in two ways: the animals were associated after death or perhaps represent living association. If the association occurred after death, the enrollment must have occurred before decay of the animal tissues. Otherwise, the hard skeletons should have been disarticulated, since dead animals always immediately are attacked by scavengers and there is almost no chance for two long-dead individuals to have been rolled together. On the other hand, if the two animals were rolled together accidentally during their life period, possibly for protection, there would seem little chance that the two individuals oriented themselves thus, parallel; head-to-head and pygidium-to-pygidium as they occur here.

The orientation of the animals suggests a volitional life association, and that the head-to-head and tail-to-tail relationship is more than a chance; if so, the easiest explanation is that they record copulation. This orientation during the sex act would correspond to that well demonstrated in modern Xiphosura where the



Text-fig. 59: Acidaspis cincinnatiensis Meek. Two individuals lying facing each other as if they are in copulation. A, dorsal view of small individual; B, dorsal view of a large individual; C, side view of both A and B individuals; note coincidence cephalon to cephalon and pygidium to pygidium. (Drawings made from photographs.)

smaller male lies over the larger female while depositing the milt. The enrollment of the two animals may well have been caused by fright or excitement during the mating period, and the two individuals became enrolled from their originally extended natural position into the cone-in-cone form now seen.

2. Acidaspis cincinnatiensis Meek (pl. 4, figs. 24-27, and text-fig. 59A-C). The specimen is 20.1 mm. in length, 13.8 mm. wide at the mid-length, and 5.6 mm. in thickness. It shows two different-sized individuals lying with venters opposed, head-to-head, and pygidium-to-pygidium. The articulated thorax and pygidium of the smaller individual is 14.9 mm. long. The larger individual measures 15.3 mm. over a comparable area (both measurements are from the first axial ring to the posterior pygidial margin). In the small individual the cephalon is present, but slightly displaced; it is lost in the large one.

The venter-to-venter orientation of these two sized individuals of the same species is highly suggestive of sexual cojugation. Perchance the digitate pygidia spines were inter-locked as clasping devices during conjugation, whether fertilization was external or internal. Such a copulatory position is common among arthropods. Which size variant correlates with which sex is problematic, although present data suggest that the male is the larger form (see p.

The conjugation of Recent arthropods is highly variable, even in closely related forms. Both of the inferred sex act positions of Flexicalymene and Acidaspis are illustrated by different species of living decapod crabs: e.g., Cancer borealis Stimpson and Callinectes

sapidus Rathbum, common decapods along the East Coast of the United States. In the first crab the smaller female, is held by the male, in a position facing each other, like the position of the Acidaspis specimen, whereas in C. sapidus the male mounts the female, as in the Flexicalymene example.

In any event in the three specimens of trilobites thus far known which possibly record the copulatory position, the specimens are dimorphic. Quite possibly much more material reposes in public and private hands and should be reported.

Figured specimens. Flexicalymene meeki (Foerste), U.C.M. 23263.
Acidaspis cincinnatiensis Meek, U.C.M. 38729.

REFERENCES

Åkesson, B., 1961, On the histological differentiation of the larvae of Pisione remota(Pisionidae, Polychaeta): Acta Zoologica, Bd. 42, no. 3, p. 177-226.

_____, 1962, The embryology of Tomopteris helgolandiaca (Polychaeta): Acta Zoologica, Bd. 43, no. 2-3, p. 135-199.

_____, 1963, The comparative morphology and embryology of the head in scal worms (Aphroditidae, Polychaeta): Arkiv för Zoologi, Bd. 16, no. 7, p. 125-163.

_____, 1966, The embryology of the polychaete Eunice koiensis: Acta Zoologica, Bd. 48, no. 1-2, p. 141-192.

_____, 1967a, On the biology and larval morphology of Ophryotrocha paerilis Claparid and Metschnikov (Polychaeta): Ophelia, vol. 4, p. 110-119.

_____, 1967b, On the nervous system of the Lopadorhychus larva (Polychaeta): Arkiv för Zoologi, Bd. 20, no.2, p. 55-58.

Anderson, D. T., 1959, The embryology of the polychaete Scoloplos armiger: Quart. Jour. Microbiol. Sci., vol. 100, p. 86-166.

_____, 1961, The development of the polychaete Haploscoloplos fragilis: Quart. Jour. Microbiol. Sci., vol. 102, p. 257-272.

_____, 1966, The comparative embryology of the Polychaeta: Acta Zoologica, Bd. 42, p. 1-39.

Angelin, N.P., 1878, Paleontologis Scandinavica: Crustacea formationis transitionis: Halmiae Fasc. 1, 2, (Stockholm).

Ashworth, J. H., 1904, Arenicola (the lug-worm) marina: Biol. Committee, Liverpool, L.M.B.C., 11.

Barnes, R. D., 1963, Invertebrate Zoology: W. B. Sanders Co., Philadelphia.

Barrange, Joachim, 1852, Systéme Silurien du Centre de La Bohême: Iére partie, Crustacés, Trilobites: v. 1, 935 p. (Prague and Paris).

Bassler, R. S., 1915, Bibliographic index of American Ordovician and Silurian fossils: Smith. Inst., United States National Museum, Bull. 92.

_____, 1919, Cambrian and Ordovician Formations of Maryland: Maryland Geol. Surv., Special Publication, p. 332-362.

Beecher, C. E., 1895a, The larval stages of Trilobites: American Geol., vol. 16, p. 166-197.

_____, 1895b, Further observation on the Ventral structures of Triarthrus: Amer. Geol., vol. 19, p. 91-100.

_____, 1897, Outline of a Natural Classification of trilobites: American Jour. Sci., vol. 3, no. 49, p. 89-106, 181-207.

Bell, W. C. and Ellinwood, H. L., 1962, Upper Franconian and Lower Trempealeauan Cambrian trilobites and brachiopods of the Wilberns Formation, Central Texas: Jour. Paleo., vol. 36, no. 3, p. 385-423.

Bookhout, C. G., 1957, The development of Dasybranchus caducua (Grabe) from the egg to the preadult: Jour. of Morphology, vol. 100, no. 1, p. 141-186.

_____, 1964, Salinity effects on the larval development of Pagurus bernhardus (L.), reared in the laboratory: Ophelia, vol. 1, no. 2, p. 275-294.

Bookhout, C. G., and Horn, Ed. C., 1949, The development of Axiothella mucosa (Andrews): Jour. of Morphology, vol. 84, no. 1, p. 145-183.

Bookhout, C. G., and Costlow, J. D., Jr., 1959, Feeding, moulting, and growth in barnacles: Friday Harbor Symposia, University of Washington Press, p. 212-225, (Seattle).

Brooks, H. K., 1957, Chelicerata, Trilobitomorpha, Crustacea (exclusive of Ostracoda), and Myriapoda: Geol. Soc. of America, Mem. 67, p. 895-930.

Butt, F. H., 1960, Arthropod head development: Biol. Rev., (Cambridge Philos. Soc.), vol. 35, no. 1, p. 43-91.

Butts, C., 1941, Geology of the Appalachian valley in Virginia: Virginia Geol. Sur., Bull. 52, pt. 2, p. 73-95.

Caster, K. E., 1938, A restudy of Paramphibius: Jour. Paleo., vol. 12, no. 1, p. 3-60.

Caster, K. E., Dalvé, E. A., and Pope, J. K., 1961, Elementary guide to the fossils and strata of the Ordovician in the vicinity of Cincinnati, Ohio: Cincinnati Mus. of Nat. History, Cincinnati, Ohio.

Comstock, J. H., 1925, Introduction to Entomology: The Comstock Pub. Co., Ithaca, N. Y.

Costello, D. D., et al., 1957, Methods for obtaining and handling marine eggs and embryos: Marine Biol. Lab., Woods Hole, Massachusetts.

Clark, R. B., 1964, Dynamics in metazoan evolution: Clarendon Press, Oxford.

Cobbold, E. S., 1931, Additional fossils from the Cambrian rocks of Comley, Shropshire: Geol. Soc. London, Quart. Jour., vol. 87,

p. 459-511.

Cooper, B., 1953, Trilobites from the Lower Champlainian Formation of the Appalachian valley: Geol. Soc. of America, Mem. 55.

Costlow, J. D., Jr., and Bookhout, C. G., 1957, Larval development of Balanus eburneus in the laboratory: Biol. Bull., vol. 112, no. 3, p. 313-324.

_____, 1958a, Moulting and respiration in Balanus amphitrite var. denticulata Broch: Physiological Zool., vol. 31, no. 4, p. 271-280.

_____, 1958b, Larval development of Balanus amphitrite var. denticulata Brock, reared in the Laboratory: Biol. Bull., vol. 114, no. 3, p. 284-295.

_____, 1959, The larval development of Callinectes sapidus Rathbun, reared in the Laboratory: Biol. Bull., vol. 116, no. 3, p. 373-396.

_____, 1960, The complete larval development of Sesarma cinerum (Bosc), reared in the Laboratory: Biol. Bull., vol. 118, no. 2, p. 203-214.

Chandonneret, J., 1950, La morphologie céphalique de Thermobia domestica (Packard): Ann. Sci. not. Zool. (II), 12, p. 145.

Costlow, J. D., Jr., Bookhout, C. G., and Monroe, R. R., 1960, The effect of salinity and temperature of larval development of Sesarma cinerum (Bosc), reared in the laboratory: Biol. Bull., vol. 118, no. 2, p. 183-202.

Cumings, E. R., 1907, The stratigraphy and paleontology of the Cincinnati series of Indiana: Indiana Dept. Geol. Nat. Res., 32nd Ann.

Rpt., p. 1060.

Dahl, E., 1958, The ontogeny and comparative anatomy of some proto-cerebral sense organ in notostracan phyllopods: Microbiological Soc., Quart. Jour., vol. 100, p. 445-462.

_____, 1963, Main evolution lines among recent Crustacea (Phylogeny and evolution of Crustacea): Mus. of Comp. Zool., Special Publ., p. 1-15.

Dalvè, E. A., 1948, The fossil fauna of the Ordovician in the Cincinnati region: Univ. of Cincinnati, Geol. Museum., Publ., Cincinnati, Ohio.

Dales, P., 1963, Annelids: Hutchinson University Library, Hutchinson & Co., London.

Dean, W. F., 1960, The Ordovician trilobite faunas of the South Shropshire I: British Mus. Bull. Geol., vol. 4, no. 4, London.

Deiss, Ch. , 1939, Cambrian stratigraphy and trilobites of north-western Montana: Geol. Soc. America, Spec. Paper 18, p. 1-131.

Deland, C. R. and Show, A. B., 1956, Upper Cambrian trilobites from western Wyoming: Jour. Paleo., vol. 30, no. 3, p. 543-562.

Dekay, J. E., 1824, Observation on the structure of trilobites and description of an apparently new genus: Lyceum Nat. Hist., New York Annals, vol. 1, pt. 1, p. 174-189.

Dobkin, S., 1961, Early developmental stages of the pink shrimp, Penaeus duorarum from Florida water: Fishery Bull. 190, vol. 61, p. 321-348.

Endo, R., 1935, The post-embryonic development of Blackwelderia quadrate Endo: Imp. Acad. Tokyo Proc., vol. 15.

Endo, R., and Resser, C. E., 1937, The Sinian and Cambrian Formations and fossils of southern Manchuria: Manchurian Sci. Mus. Bull., 1.

Evitt, W. R., 1961, Early ontogeny in the trilobite family Asaphidae: Jour. Paleo., vol. 35, no. 5, p. 986-995.

Evitt, W. R., and Whittington, H. B., 1953. The exoskeleton of Flexicalymene (Trilobita): Jour. Paleo., vol. 27, no. 1, p. 49-55.

Fage, L., 1949, Classe des Merostomaces: Traite de Zoologis, Tome VI, p. 219-262 (Paris).

Fraser, J., 1962, Nature Adrift: G. T. Foulis & Co., Ltd., London.

Fränsemier, L., 1939, Zür Frage der Herkunft des Metanauplialen Mesoderms und die Segmentbilding bei Artemia salina Leach: Zeitschr. Wiss. Zool., vol. 152, p. 439-472.

Frederichson, E. A., 1948, Upper Cambrian trilobites from Oklahoma: Jour. Paleo., vol. 22, no. 6, p. 798-803.

Foerste, A. F., 1909, Preliminary notes on Cincinnatian and Lexington fossils: Denison University, Jour. of Sci. Lab. Bull., vol. 14, p. 294.

_____, 1919-1921, Notes on Isotelus, Acrolichis, Calymene, and Encrinurus: Denison University, Jour. of Sci. Lab. Bull., vol. 19, p. 65-81.

Ford, S. W., 1877, On some embryonic forms of trilobites from the primordial rock of Troy, N. Y.: American Jour. of Sci., Ser. 3, vol. 22, p. 250-259.

Grant, R. E., 1965, Fauna and stratigraphy of the Snow Range Formation (Upper Cambrian) in southwestern Montana and northeastern Wyoming: Geol. Soc. America, Mem. 96.

Green, J., 1832, Trilobites of North America: No. 12, Joseph Brano Co., Philadelphia, Pa., p. 1-93.

Green, J., 1961, A Biology of Crustacea: H. F. & G. Witherby, Ltd.

Hall, J., 1847, Paleontology of New York (Containing descriptions of the organic remains of the lower division of the New York system): Nat. History of New York, Paleo., vol. 1, p. 231.

Hanson, E. D., 1964, Animal diversity (Foundation of Modern Biology Series): Prentice-Hall, Inc., New York.

Hanström, B., 1928, Vergleichede Anatomie des Nervensystems der wirbellosen Tiere: Berlin.

Harrington, H. J., 1956, Olenellidae and advanced cephalic spines: Jour. Paleo., vol. 30, no. 1, p. 56-61.

_____, 1959, General description of Trilobita (Treatise on Invertebrate Paleontology, Arthropoda, pt. O): Geol. Soc. American and Univ. of Kansas Press, p. 38-117.

Harrington, H. J., and Kay, M., 1951, Cambrian and Ordovician faunas of eastern Colombia: Jour. Paleo., vol. 25, no. 5, p. 655-668.

Harrington, H. J., and Leanza, F., 1957, Ordovician trilobites of Argentina: Univ. of Kansas, Dept. of Geology, Spec. Publication 1.

Hartman, O., 1945, The Marine annelids of North Carolina: Duke Univ. Press, Bull. no. 2, p. 1-54.

Henningsmoen, G., 1951, Remarks on the Classification of trilobites: Norsk geol. Tidsskr., Bd. 29, p. 174-217 (Oslo).

_____, 1957, The trilobite family Olenidae: Norsk Vidensk. Akad., Skr., 1 Kl., no. 1, (Oslo).

_____, 1958, The Upper Cambrian faunas of Norway; with descrip-

tion of non-olenid invertebrate fossils: Norsk geol. Tidsskr., Bd. 38, p. 179-196 (Oslo).

_____, 1964, Zig-Zag Evolution: Norsk geol. Tidsskr., Bd. 44, p. 341-352.

Herriksen, K. L., 1926, The segmentation of the trilobites head: Dansk geol. Foren., Medd., vol. 7, p. 1-32 (Køben havn).

Herskowitz, I. H., 1962, Genetics: Little Brown and Co., Boston.

Hintz, L. F., 1952, Lower Ordovician trilobites from western Utah and eastern Nevada: Univ. Utah, Bull. 48, p. 1-249.

Hofmann, T. F., and R. L. Parsley, 1966, Antennae of Ogygopsis: Jour. Paleo., vol. 40, no. 1, p. 208-211.

Holm, G. and Westergård, A. H., 1930, A Middle Cambrian fauna from Bernett Island: Acad. Sci., U.S.S.R., Mem. 8 (Phy.-Math,, Class, vol. 21, no. 2).

Horn, E. C., and Bookhout, C. G., 1950, The early development of Haploscoloplos bustoris (Eisig): Jour. Elisha Mitchell Sci. Soc., vol. 66, no. 1, p. 1-9.

Howell, B. F., 1925, The faunas of the Cambrian Paradoxides beds at Manuels, Newfoundland: Bull. American Paleontology, vol. 2, no. 43, p. 9-140.

Howell, B. F., and Duncan, D., 1939, Middle-Upper Cambrian transition faunas in North America: Wagner Free Inst. Sci., Bull., vol. 14, no. 1.

Howell, B. F. et al., 1947, Terminology for describing Cambrian trilobites: Jour. Paleo., vol. 21, no. 1, p. 72-76.

Hu, C. H., 1963, The dimorphism and ontogeny of Norwoodella halli

Resser: Paleo. Soc. Japan, Proc. Trans., no. 52, p. 129-132.

_____, 1964, The ontogeny and dimorphism of Welleraspis lata Howell (Trilobita): Jour. Paleo., vol. 38, no. 1, p. 95-97.

Hunt, A. S., 1967, Growth variation and instar development of an agnostid trilobite: Jour. Paleo., vol. 41, no. 1, p. 203-208.

Hupé, P., 1950, Étude statistique de l'évolution du cephalon chez les Trilobites, Proparia et Opistoparia: Soc. Géol. France, Bull., 5 Sér., t. 20, p. 9-24.

_____, 1951, Sur les affinités des Trilobites: Soc. Géol. France, Bull., 6 Sér., vol. 1, p. 469-486.

_____, 1953a, Classe des trilobites: Traité de paléontologie, vol. 3, p. 44-246 (Paris).

_____, 1953b, Quelques rémarques sur la croissance et la segmentation des Trilobitea: Soc. Géol. France, Bull., 6 Sér., vol. 3, p. 3-11.

_____, 1953c, Contribution a l'étude du Cambrien inférieur et du précambrien III de l'Anti-Atlas marocain: Serv. géol. Maroc, Notes et Mém., 103, p. 1-402.

_____, 1954, Classifaction de Trilobites: Ann. Paléo., vol. 4, p. 91-325.

Ishibashi, E., et al., 1938, General Zoology: Kasho Book Co., Tokyo. (In Japanese).

Iwanoff, P. P., 1933, Die embryonale Entwicklung von Limulus moluccanus: Zool. Jahrb. Bd. 56, Abt. f., Anat. 2, p. 164-346.

_____, 1944, Primary and secondary metamery of the body: Jour. Gen. Biology, Moscow, 5, (Russian with English summary).

Jaanusson, V., 1954, Zur Morphology und Taxonomie der Illaeniden: Arkiv för Mineral. och Geol., Kungl. Svenska Vet.-akad., no. 20, p. 545-583.

Johansson, G., 1932, Beiträge zur Kenntnis der Morphologie und Entwicklung des Gehirn von Limulus polyphemus: Acta Zoologica, Bd. 14, p. 1-79. (Stockholm).

Kingsley, J. S.,1892-3,The embryology of Limulus: Jour. Morph., vol. 7 and 8, no. 1 and 2, p. 35-66 and 196-260.

_____, 1897, The systematic position of the trilobites: The American Geol., vol. 20, p. 33-40.

Kobayashi, T., 1935, The Cambro-Ordovician Formations and faunas of South Choesen: Imp. Univ. Tokyo, Jour. Fac. Sci., Sec. II, vol. 4, pt. 2, p. 1-344.

_____, 1936, On the Parabolinella fauna from province Jujuy, Argentina with a note on the Olenidae: Japanese Jour. Geol. and Geog., vol. 13, no. 1-2, p. 85-102.

_____, 1939a, On the agnostids (part 1): Imp. Univ. Tokyo, Jour. Faculty Sci., Sec. II, vol. 5, pt. 5, p. 72-192.

_____, 1939b, Supplementary notes on the Agnostida: Geol. Soc. Japan, Jour., vol. 46, no. 554, p. 97-100.

_____, 1944, On the Eodiscids: Imp. Univ. Tokyo, Jour. Fac. Sci., Sec. II, vol. 7, pt. 1, p. 1-74.

_____, 1960a, Notes on the natural classification of Trilobita: Jour. of Geol. Soc. Japan., vol. 66, no. 776, p. 538-546 (in Japanese).

_____, 1960b, Studies on trilobites in last three decades

(Presidential Address): Paleo. Soc. (Japan), Trans.-Proc., no. 37, p. 230-237.

_____, 1960c, The Cambro-Ordovician Formations and faunas of South Korea, part 7: Univ. Tokyo, Jour. Fac. Sci., Sec. II, vol. 12, pt. 2, p. 329-420.

_____, 1962, The Cambro-Ordovician Formation and faunas of South Korea, part 9: Univ. Tokyo, Jour. Fac. Sci., Sec. II, vol. 14, pt. 1, p. 1-152.

Kobayashi, T. and Kato, F., 1951, On the ontogeny and ventral morphology of Redlichia chinensis with description of Alutella nakamurai, new gen. and sp.: Univ. Tokyo, Jour. Fac. Sci., Sec. II, vol. 8, pt. 3, p. 99-143.

Lankester, E. R., 1904, The structure and classification of the Arachinida: Quart. Jour. Microbiological Sci., vol. 48, pt. 2, p. 165-269.

Lever, W., 1966, New criteria for ascertaining sex in Oncopeltas fasciatus (Dallus): Turtox News, vol. 44, no. 2, p. 62-63.

Lillie, R. S., 1905, The structure and development of the nephrida of Arenicola cristata Stimpson: Zool. Station, Mitt., Neapel. vol. 17, p. 341.

Lindström, G., 1901, Research on the visual organ of trilobites: Kungl. Svenska Vet.-Akad., Handl., Bd. 34, no. 8, p. 1-89.

Lochman, C., 1940, Fauna of the basal Bonneterre dolomite (Upper Cambrian) of southeastern Missouri: Jour. Paleo., vol. 14, no. 1, p. 1-53.

_____, 1950, Upper Cambrian faunas of the Little Rocky Mountains,

Montana: Jour. Paleo., vol. 24, no. 3, p. 322-349.

_____, 1952, Cambrian stratigraphy and paleontology near Caborca, northwestern Sonora, Mexico: Smith. Misc. Coll., vol. 119, no. 1.

_____, 1956a, The evolution of some Upper Cambrian and Lower Ordovician trilobites families: Jour. Paleo., vol. 3, no. 3, p. 889-896.

_____, 1956b, Stratigraphy, paleontology, and paleogeography of the Elliptocephala, Asaphoides strata in Cambrian and Hoosick Quadrangles, New York: Geol. Soc. Amer. Bull., vol. 67, p. 1331-1396.

_____, 1964a, Basal Ordovician faunas from the Williston Basin, Montana: Jour. Paleo., vol. 38, no. 3, p. 453-476.

_____, 1964b, Upper Cambrian faunas from the subsurface Deadwood Formation, Williston Basin, Montana: Jour. Paleo., vol. 38, no. 1, p. 33-60.

_____, 1966, Lower Ordovician (Arenig) faunas from the Williston Basin, Montana and North Dakota: Jour. Paleo., vol. 40, no. 3, p. 512-548.

Lochman, C. Duncan, D., 1944, Early Upper Cambrian faunas of Central Montana: Geol. Soc. Amer., Spec. Paper no. 4, p. 1-181.

Lochman, C., and Hu, C. H., 1959, A Ptychaspis faunule from the Bear River Range, southeastern Idaho: Jour. Paleo., vol. 33, no. 3, p. 404-427.

_____, 1960, Upper Cambrian faunas from the northwest Wind River Mts., Wyoming, Pt. I: Jour. Paleo., vol. 34, no. 5, p.

793-834.

_____, 1961, Upper Cambrian faunas from the northwest Wind River Mts., Wyoming, Pt. II: Jour. Paleo., vol. 35, no. 1, p. 125-146.

_____, 1962a, Upper Cambrian faunas from the northwest Wind River Mts., Wyoming, Pt.III: Jour. Paleo., vol. 36, no. 1, p. 1-28.

_____, 1962b, An Aphelaspis zone faunule from Logan, Montana, Jour. Paleo., vol. 36, no. 3, p. 431-441.

Lochman, C. and Wilson, J. L., 1958, Cambrian biostratigraphy in North America: Jour. Paleo., vol. 32, no. 2, p. 312-350.

Locke, J., 1838, Isotelus maximus Locke: Geol. Surv. Ohio., 2nd Ann. Rep., p. 247.

_____, 1842, On a species of trilobite of very large size: American Jour. Sci., and Arts, vol. 45, p. 366.

Lu, Y. H., 1957, Trilobita: Index fossils of China, Acad-Sinica, Inst. Paleontology, Geol. Press, p. 249-320. Peking.

Manton, S. M., 1934, On the embryology of the crustacea Nebalia bipes: Roy. Soc. London, Philos. Trans., Ser., B, vol. 223, p. 163-238.

_____, 1949, Studies on the Onychaphora VII; The early embryonic stages of Peripatapsis and some general considerations concerning the morphology and phylogeny of the Arthropoda: Roy. Soc. London, Philos. Trans., Ser. B, vol. 233, p. 483.

_____, 1960, Concerning head development in the arthropods: Biol. Rev. (Cambridge Philos. Soc.), vol. 35, no. 2, p. 264-282.

Matthew, G. F., 1896, Faunas of the Paradoxides beds in eastern North America, no. 1: New York Acad. Sci., Trans., vol. 15, p. 192-247.

_____, 1898, Studies on Cambrian faunas. Roy. Soc. Canada, Trans.-Proc., 2nd Ser., vol. 4, Sec. 4, p. 139-141.

Meek, F. B., 1873, Fossils of the Cincinnati Group: Geol. Surv. Ohio, Report, vol. 1, pt. 2, p. 1-243

Miner, R. W., 1950, Field Book of seashore life: G. P. Putnam's Sons, New York.

Nelson, C. A., 1951, Cambrian trilobites from the St. Croix valley: Jour. Paleo., vol. 25, no. 6, p. 765-784.

Nickles, J. M., 1902, The geology of Cincinnati: Jour. Cincinnati Soc. Nat. Hist., vol. 20, no. 2, p. 49-100.

Öpik, A. A., 1952, The hypostoma of Pagetia: Jour. Paleo., vol. 26, no. 2, p. 272-274.

_____, 1958, The Cambrian trilobite Redlichia organization and generic concept: Australia Dept. Nat. Develop., Bureau Min. Res. Geol. and Geog., Bull., no. 42, p. 5-37.

Parkard, A. S., 1870, The development of Limulus polyphemus: Boston Soc. Nat. Hist., Ann. Mem., vol. 2, p. 155-202.

_____, 1880a, Anatomy, Histology, and embryology of Limulus polyphemus: Boston Soc. Nat. Hist., Ann. Mem., vol. 2, p. 1-45.

_____, 1880b, Further studies on the brain of Limulus polyphemus with notes on its embryology: Nat. Acad. of Sci. 8th Mem., vol. 6, p. 287-331.

Palmer, A. R., 1954, The fauna of the Riely Formation in Central Texas: Jour. Paleo., vol. 28, no. 6, p. 710-782.

_____, 1955, Upper Cambrian Agnostidae of the Eureka district, Nevada: Jour. Paleo., vol. 29, no. 1, p. 86-101.

_____, 1957, Ontogenetic development of two olenellid trilobites: Jour. Paleo., vol. 31, no. 1, p. 105-128.

_____, 1958, Morphology and ontogeny of a Lower Cambrian ptychoparid trilobite from Nevada: Jour. Paleo., vol. 32, no. 1, p. 154-170.

_____. 1960, Trilobites of the Upper Cambrian Dunderberg Shale, Eureka district, Nevada: United State Geol. Surv., Prof. paper 334-C.

_____, 1962, Comparative ontogeny of some opisthoparian, gonatoparian, and proparian, Upper Cambrian trilobites: Jour. Paleo., vol. 36, no. 1, p. 87-96.

_____, 1964, An unusual Lower Cambrian trilobite fauna from Nevada: United States Geol. Surv., Prof. paper 483-F.

_____, 1965, Trilobites of the Late Cambrian pterocephaliid Biomer in the Great Basin, United States: United States Geol. Surv., Prof. paper 493.

Patten, W., 1889, Segmental sense-organ of arthropods: Jour. Morph., vol. 2, no. 3, p. 600-602.

_____, 1896, Variation in the development of Limulus polyphemus: Jour. of Morph., vol. 12, no. 1, p. 21-100.

_____, 1912, The evolution of the vertebrates and their kin: Philadelphia, Pa., 215-248.

Poulsen, C., 1923, Bornholms Olenuslag og deres fauna: Danm. Geol. Unders, vol. 2, no. 40, p. 1-83.

_____, 1932, The Lower Cambrian fauna of East Greenland: Danm. Geol. Unders, vol. 87, no. 6, p. 1-16.

Poulsen, V., 1964, Contribution to the Lower and Middle Cambrian paleontology and stratigraphy of northwest Greenland: Medd. om Grønland, Bd. 164, no. 6, p. 1-45.

Pocock, R. I., 1902, The taxonomy of recent species of Limulus: Ann. and Magazine of Nat. Hist., Ser. 7, vol. 9, p. 256-266.

Přibyl, A., 1949, Studies O trilobitech Nadčeldi Odontopleuracea nov. superfam: Rozpravy Státuího Geol., Ŭstavu Rep. Československe Svazek, 12, p. 117.

Raasch, G. C., and Lochman, C., 1945, Crepicephalus edwardi Raasch, new name for Crepicephalus oweni Raasch, 1953: Jour. Paleo., vol. 19, no. 1, p. 77.

Rasetti, F., 1944, Upper Cambrian trilobites from the Lévis conglomerate: Jour. Paleo., vol. 18, p. 229-258.

_____, 1945a, New Upper Cambrian trilobites from the Lévis conglomerate: Jour. Paleo., vol. 19, p. 462-478.

_____, 1945b, Fossiliferous horizon in the "Sillery Formation" near Lévis, Quebec: American Jour. Sci., vol. 243, no. 6, p. 305-319.

_____,1945c, Evolution of the facial sutures in the trilobites Loganopeltoides and Loganopeltis: American Jour. Sci., vol. 243, p. 44-50.

_____, 1948a, Lower Cambrian trilobites from the Conglomerate of Quebec: Jour. Paleo., vol. 22, no. 1, p. 1-24.

_____, 1948b, Cephalic structures in Loganpeltoides and the origin of "Hypoparian" trilobites: Jour. Paleo., vol. 22, no. 1, p. 25-29.

_____, 1951, Middle Cambrian stratigraphy and faunas of the Canadian Rocky Mountains: Smith Misc. Coll., vol. 116, no. 5, p. 1-271.

_____, 1952a, Ventral cephalic sutures in Cambrian trilobites: American Jour. Sci., vol. 250, p. 885-898.

Raw, F., 1925, The development of Leptoplastus salteri and other trilobites: Geol. Soc. London, Quart. Jour., vol. 81, p. 223-324.

_____, 1927, The ontogeny of trilobites and their significance: American Jour. Sci., Ser. 5, no. 14, p. 7-35, and 131-149.

_____, 1937, Systematic position of the Olenellidae (Mesonacidae): Jour. Paleo., vol. 11, no. 7, p. 575-597.

_____, 1952, A note on Ross' "ontogenies of three Garden City (Early Ordovician) trilobites": Jour. Paleo., vol. 25, no. 5, p. 854-858.

_____, 1953, The external morphology of the trilobite and its significance: Jour. Paleo., vol. 27, no. 1, p. 82-129.

Raymond, P. E., 1917, Beecher's classification of trilobites after twenty years: American Jour. Sci., vol. 43, p. 196-210.

_____, 1920a, Phylogeny of the Arthropoda with especial reference to the trilobites: American Nat., vol. 54, p. 398-413.

_____, 1920b, The appendages, anatomy, and relationships of trilobites: Connecticut Acad. of Arts. and Sci., Mem. vol. 7, p. 1-163.

_____, 1921, Criteria for species, phylogenies, and faunas of trilobites: Geol. Soc. America, Bull., vol. 32, p. 349-352.

Resser, C. E., 1928, Cambrian fossils from the Mohove desert: Smith.

Misc. Coll., vol. 81, no. 2, p. 1-14.

_____, 1936, Second contribution to nomenclature of Cambrian trilobites: Smith. Misc. Coll., vol. 95, no. 4, p. 1-29.

_____, 1937, Third contribution to nomenclature of Cambrian trilobites: Smith. Misc. Coll., vol. 95, no. 22, p. 1-29.

_____, 1938, Cambrian system (restricted) of the southern Appalachians: Geol. Soc. America, Spec. Paper, no. 15, p. 16.

_____, 1939, The Ptarmigania strata of the north Wasatch Mountains: Smith. Misc. Coll., vol. 98, no. 24, p. 1-72.

Resser, C. E. and Howell, B. F., 1938, Lower Cambrian Olenelus zone of the Appalachians: Geol. Soc. America, Bull., vol. 49, p. 195-248.

Robinson, R. A., 1964, Late Middle Cambrian faunas from western Utah: Jour. Paleo., vol. 36, no. 3, p. 510-566.

_____, 1967, Ontogeny of Bathyuriscus fimbriatus and its bearing on affinitives of Corynexochid trilobites: Jour. Paleo., vol. 41, no. 1, p. 213-221.

Ross, R. J., Jr., 1951a., Stratigraphy of the Garden City Formation in northeastern Utah and its trilobite faunas: Peabody Mus. Nat. Hist. Yale Univ., Bull. 6, p. 1-157.

_____, 1951b, Ontogeny of three Garden City (Early Ordovician) trilobites: Jour. Paleo., vol. 25, p. 578-586.

_____, 1953, Additional Garden City (Early Ordovician) trilobites: Jour. Paleo., vol. 27, no. 5, p. 633-646.

_____, 1967, Calymene and other Ordovician trilobites from Kentucky and Ohio: United States Geol. Surv., Prof. paper 583-B.

Rozova, A. V., 1964, Biostratigraphy and morphology of trilobites from the Lower and Middle Cambrian of the northwestern Siberia platea: Acad. Sci. of U.S.S.R., vol. 5, p. 1-97.

Ruedemann, R., 1926, Utica and Lorraine Formation of New York part 2: New York State Mus., Bull. no. 272, p. 106-137.

Sanders, H. L., 1957, Cephalocarida and crustacean phylogeny: Systematic Zool., 6, (Ser. 3), p. 112-128.

_____, 1959, The significance of the Cephalocarida in crustacean phylogeny: International Cong. Zool. 15th Session, London (1958), Proc., p. 337-340.

_____, 1963a, Significance of the Cephalocarida phylogeny and evolution of Crustacea: Mus. Comp. Zool. Special publication, p. 163-177.

_____, 1963b, The Cephalocarids; Functional morphology, larval development, comparative external anatomy: Connecticut Acad. Arts and Sci., Mem., vol. 15, p. 1-43.

Sanders, H. L., and Hessler, R. P., 1963, The larval development of Lightiella incisa Gooding (Cephalocarida): Crustaceana, vol. 7, p. 82-96.

Saito, I., 1934, Older Cambrian trilobites and Conchostraca from North Western Korea: Japanese Jour. Geol. and Geog., vol. 11, no. 3-4, p. 211-237.

Segrove, F., 1941, The development of the serpuli Pomatoceros triqueter L.: Quart. Jour. Micr. Sci., vol. 82, p. 467-540.

Shino, S. M., 1950, Studies on the embryonic development of Panulirus japanicus (von Siebold): Univ. Mie, Jour. Faculty of Fishery,

vol. 1, no. 1, p. 1-168, (Japan).

Shaw, A. B., 1951, The paleontology of northwestern Vermont, part I; New Late Cambrian trilobites: Jour. Paleo., vol. 25, no. 1, p. 97-114.

_____, 1956a, A Cambrian Aphelaspis fauna from Steel Butte near Boulder, Wyoming: Jour. Paleo., vol. 30, no. 1, p. 48-52.

_____, 1956b, Quantitive trilobite studies, part 1; The statistical description of trilobites: Jour. Paleo., vol. 30, no. 5, p. 1209-1224.

_____, 1966, Paleontology of northwestern Vermont, part XII; Fossils from the Ordovician Highgate Formation: Jour. Paleo., vol. 40, no. 6, p. 1312-1329.

Shuster, C. N., 1950, Observation on the natural history of the American horse-shoe crab Limulus polyphemus: Woods Hole Oceanographic Institution, Contribution no. 564, p. 18-23.

_____, 1955, On morphometric and serological relationships within the Limulidae with particular reference to Limulus polyphemus (L.): Dissertation Abstracts, vol. 18, no. 2, p. 1-287 (1958).

_____, 1960, Xiphosura: Encyclopedia of Science and Technology, McGraw Hill Book Co., Inc., New York. 14, p. 563-567.

Siewing, R., 1963, Studies in Malcostracan morphology; Phylogeny and evolution of Crustacea: Mus. Comp. Zool., Spec. Publication, p. 85-110.

Snajdr, M., 1958, Trilobiti; Českého Středniho Kambria: Nakladatelestvi Ceskoslovenské Adad., Svazek 24, p. 1-237.

Snodgrass, R. E., 1938, Evolution of the Annelida, Onychophora, and Arthropoda: Smith. Misc. Coll., vol. 97, no. 6, p. 1-149.

_____, 1952, A text-book of arthropod anatomy: Comstock Publishing Assoc., Cornell Univ. Press, Ithaca, New York.

_____, 1956, Crestacean metamorphoses: Smith. Misc. Coll., vol. 131, no. 10, p. 1-73.

Sollaud, E., 1923, Recherches sur l'embryogénie des Crustacés décapods de la sousfamille des "Palemoninae": Biol. France et Belgique, Bull., vol. 5, p. 234.

Slocom, A. W., 1916, Trilobites from the Maquaketa beds Fayette County, Iowa: Iowa Geol. Surv., Ann. Report, vol. 25, (for 1914), p. 183-250.

Storer, T. I., 1943: General Zoology: McGraw-Hill Book Co., Inc., New York.

Størmer, L., 1930, Scandinavian Trinucleidae: Norsk Vidensk.-Akad., Skr., 1 Kl., Bd. 4, p. 1-105 (Oslo).

_____, 1942, Studies on trilobite morphology. Part II; The larval development, the segmentation, and the natures, and their bearing on trilobite classification: Norsk geol. Tidsskr., Bd. 21, p. 49-164.

_____, 1944, On the relationships and phylogeny of fossil and recent Arachnomorpha: Norsk Vidensk.-Akad., 1 Kl., Bd. 5, p. 1-153.

_____, 1949, Classe Trilobita: Traité de Zoologie, vol. 6, p. 159-197 (Paris).

_____, 1951, Studies on trilobite morphology, Part III: The ventral cephalic structure with remarks on the zoological position

of the trilobites: Norsk geol. Tidsskr., Bd. 29, p. 108-158.

_____, 1952, Phylogeny and taxonomy of fossil horseshoe crabs: Jour. Paleo., vol. 26, no. 4, p. 630-636.

_____, 1955, Merostomata (Treatise on Invertebrate Paleontology; Arthropoda 2, part P): Geol. Soc. America and Univ. of Kansas Press, p. 4-41.

Strand, T., 1927, The ontogeny of Olenus gibbosus: Norsk geol. Tidsskr., Bd. 9, no. 3-4, p. 320-329.

Stubblefield, C. J., 1926, Notes on the development of a trilobite, Shumardia pusilla (Sars): Linn. Soc. Zool. London, Jour., vol. 36, p. 345-372.

_____, 1936, Cephalic sutures and their bearing on current classification of trilobites: Biol. Rev. (Cambridge Philos. Soc.), vol. 11, p. 407-440.

Stumm, E. and Kauffman, E. G., 1958, Calymenid trilobites from the Ordovician rocks of Michigan: Jour. Paleo., vol. 32, no. 5, p. 943-960.

Tasch, P., 1952, Adaptive trend in eye-line development in the Olenellidae: Jour. Paleo., vol. 26, no. 3, p. 484-488.

Temple, J. T., 1952, The ontogeny of the trilobite Dalmanitina olini Geol. Mag., vol. 86, no. 4, p. 251-262.

Thorson, G., 1946, Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the Soung (Øresund): Komm. Danmarks Fiskeri-og Havunders., Medd., Ser. Plankton, 4, no. 1, p. 1-523.

Tiegs, O. W., and Manton, M., 1958, The evolution of the arthropods:

Biol. Rev. (Cambridge Philos. Soc)., vol. 33, no. 3, p. 255-337.

Tripp, R. P., 1958, Stratigraphical and geographical distribution of the named species of the trilobites superfamily Lichacea: Jour. Paleo., vol. 32, no. 3, p. 574-582.

Troedsson, G. T., 1928, On the Middle and Upper Ordovician faunas of northern Greenland. Part II; Jubilaeum ekapeditionen nord om Grønland, no. 5, p. 1920-1923. København.

Ulrich, E. O., 1878, Description of some new species of fossils from the Cincinnati Group: Cincinnati Soc. Nat. Hist., Jour., vol. 1, no. 2, p. 92-100.

_____, 1914, Isotelus covingtonesis: Cincinnati Soc. Nat. Hist., Jour., vol. 21, p. 145.

Vendel, A., 1949, Gènèralité composition de L'embranchement: Traité de Zoologie, Tome 6, p. 79-158 (Paris).

Vernberg, F. J. and Costlow, J. D., Jr., 1966, Handedness in fiddler crabs (genus Uca): Crustaceana, vol. 11, pt. 1, p. 61-64.

Walcott, C. D., 1879, The Utica slate formations. Fossils of the Utica slate and metamorphoses of Triarthrus beacke: Albany Ist. Trans., vol. 10, p. 1-38.

_____, 1881, The trilobite, new and old evidence relating to its organization: Mus. Comp. Zool., Bull., 6, p. 192-224.

_____, 1910, Cambrian geology and paleontology, Olenellus and other genera of the Mesonacidae: Smith Misc. Coll., vol. 53, no. 6, p. 231-422.

_____, 1913, New Lower Cambrian subfauna: Smith. Misc. Coll., vol. 57, no. 3, p. 316.

_____, 1914, Dikelocephalus and other genera of the Dikelocephalinae: Smith. Misc. Coll., vol. 57, no. 13, p. 346-383.

_____, 1916, Cambrian trilobites: Smith. Misc. Coll., vol. 64, no. 3, p. 155-258.

_____, 1917, Fauna of the Mount Whyte Formation: Smith. Misc. Coll., vol. 67, no. 3, p. 61-114.

_____, 1918, Cambrian geology and paleontology; Appendages of trilobites: Smith. Misc. Coll., vol. 67, no. 4, p. 115-216.

_____, 1921, Notes on Structure of Neoleus: Smith. Misc. Coll. vol. 67, no. 7, p. 365-377.

_____, 1925, Cambrian and Ozarkian trilobites: Smith. Misc. Coll., vol. 75, no. 3, p. 59-146.

Wahlenberg, G., 1821, Petrificata Telluris Syecana: Nava Acta Soc. Regiae Sci., Upsaliae, p. 1-116.

Warburg, E., 1925, The trilobite of the Leptaena limestone in Dalarne: Univ. Uppsala, Geol. Inst., Bull., vol. 17, p. 1-450.

Waterman, T. H., 1960, The physiology of Crustacea: Vol. 1 and 2. Academic Press, New York and London.

Weber, H., 1952, Morphologie, Histologie und Entwicklungeshichte der Articulaten: Fortsch. Zool., Bd. 9, p. 18-231.

Whittington, H. B., 1941a, The Trinucleidae, with special reference to North American genera and species: Jour. Paleo., vol. 15, no. 1, p. 21-41.

_____, 1941b, Silicified Trenton trilobites: Jour. Paleo., vol. 15, p. 492-522.

_____, 1954, Status of Invertebrate Paleontology, 1953: Mus. Comp. Zool., Bull., vol. 112, no. 3, p. 193-200.

_____, 1956a, Beecher's supposed odontopleurid protaspis is a phacopid: Jour. Paleo., vol. 30, no. 1, p. 104-109.

_____, 1956b, Type and other species of Odontopleuridae (Trilobita): Jour. Paleo., vol. 30, no. 3, p. 504-520.

_____, 1956c, Photographing small fossils: Jour. Paleo., vol. 30, no. 3, p. 756-757.

_____, 1956d, Beecher's lichid protaspis and Acanthopyge sonsanguinea (Trilobita): Jour. Paleo., vol. 30, no. 5, p. 1200-1204.

_____, 1956e, Silified Middle Ordovician trilobite; The Odontopleuridae: Mus. Comp. Zool., Bull., vol. 114, p. 155-288.

_____, 1957a, Ontogeny of Elliptocephala, Paradoxides, Sao, Blainia, and Triarthrus (Trilobita): Jour. Paleo., vol. 30, no. 5, p. 934-946.

_____, 1957b, The ontogeny of trilobites: Biol. Reviews (Cambridge Philos. Soc.), vol. 32, p. 421-469.

_____, 1958, Ontogeny of the trilobite Peltura scarabaeoides from Upper Cambrian, Denmark: Paleontology, vol. 1, pt. 3, p. 200-206.

_____, 1959a, Silicified Middle Ordovician trilobites: Mus. Comp. Zool., Bull., vol. 121, no. 8, p. 378-496.

_____, 1959b, Ontogeny of Trilobita (Treatise on Invertebrate Paleontology, part O, Arthropoda 1): Geol. Soc. America and Univ. Kansas Press, p. 127-144.

_____, 1963, Middle Ordovician trilobites from Lower Cow Head, western Newfoundland: Mus. Comp. Zool., Bull., vol. 129, no. 1, p. 7-119.

_____, 1965, Trilobites of the Ordovician Table Head Formation, western Newfoundland: Mus. Comp. Zool., Bull., vol. 132, no. 4, p. 281-442.

_____, 1966, Phylogeny and distribution of Ordovician trilobites: Jour. Paleo., vol. 40, no. 3, p. 696-737.

Whittington, H. B., and Evitt, W. R., 1954, Silicified Middle Ordovician trilobites: Geol. Soc. American, Mem. 59, p. 1-137.

Whittington, H. B., and Bohlin, B., 1958, New Lower Ordovician Odontopleuridae (Trilobita) from Oland: Geol. Inst. Uppsal. Bull., vol. 38, p. 37-45.

Winston, P., and Nicholl, H., 1967, Late Cambrian and Early Ordovician faunas from the Wilberns Formation of Central Texas: Jour. Paleo., vol. 41, no. 1, p. 66-96.

Williams, A., 1965, Marine decapod crustaceans of the Carolinas: Fish. Bull., vol. 65, no. 1, p. 1-271.

Wilson, J. L., 1951, Franconian trilobites of the Central Appalachians: Jour. Paleo., vol. 25, no. 5, p. 617-654.

_____, 1956, Revision in nomenclature and new species of Cambro-Ordovician trilobites from the Marathon uplift, West Texas: Jour. Paleo., vol. 30, no. 6, p. 1341-1349.

_____, 1957, Geography of olenid trilobite distribution and its influence on Cambro-Ordovician correlation: American Jour. Sci., vol. 255, p. 321-340.

Explanation of Plate 1

Figures 1-14 - Kormagnostus simplex Resser

1,6-8 - Early meraspides. 1, smallest cephalon, showing the conical glabella and the median furrow on the preglabellar field, x 53, U.C.M. 38722a; 6,7, two pygidia each associated with one thoracic segment; notice the conical pygidal axis; 6, x 35, U.C.M. 38722f; 7, x 34, U.C.M. 38722g; 8, a broken pygidium apparently without thoracic segment, x 25, U.C.M. 38722h.

2-4,9,10,12-14 - Late meraspides. 2-4, three cephala, showing the disappearance of the median furrow and the truncate-conical glabella; 2, x 32, U.C.M. 38722b; 3, x 15, U.C.M. 38722c; 4, x 17, U.C.M. 38722d; 9,10, two pygidia showing the subquadrate axial lobe; 9, x 30, U.C.M. 38722i; 10, x 29, U.C.M. 38722j; 12-14, pygidal, side, and cephalic views of an enrolled meraspis, x 17, U.C.M. 38722.

5,11 - Holaspides. 5, a cephalon, notice the anterior pits and the palpebral ridges on the sides of the glabella, x 8, U.C.M. 38722e; 11, a broken pygidium showing the broadly expanded posterior axis, x 13, U.C.M. 38722k.

Figures 15-32 - Pagetia clytia Walcott

23 - Paraprotaspis. A complete instar with no thoracic segments, x 50, U.C.M. 38723i.

15-17 - Three early meraspid pygidia. Notice the association of the thoracic segment; 15, x 39, U.C.M. 38723a; 16, x 40, U.C.M. 38723b; 17, x 40, 38723c.

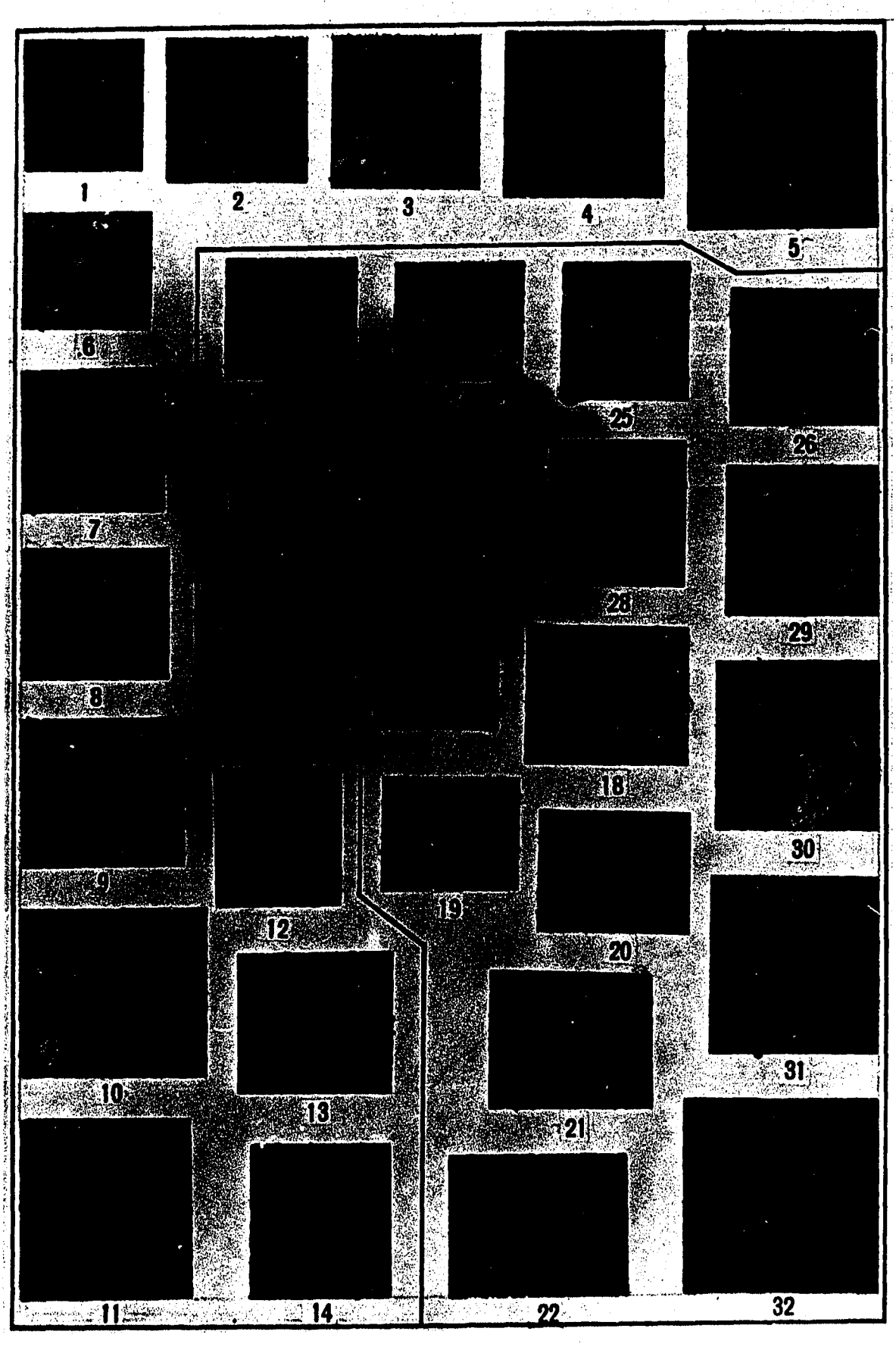
24-25 - Two early meraspid cranidia. Notice the narrower anterior border and the pair of anterior pits on the sides of the glabella; 24, x 26, U.C.M. 38723j; 25, x 26, U.C.M. 38723k.

18,19 - Two late meraspid pygidia; 18, x 25, U.C.M. 38723d; 19, x 28, U.C.M. 38723e.

26,27. - Two late meraspid cranidia. Notice the expansion of the anterior borders; 26, x 26, U.C.M. 387231; 27, x 28, U.C.M. 38723m.

20-22 - Three holaspis pygidia, showing the median tubercles on the axial rings; 20, x 13, U.C.M. 38723f; 21, x 14, U.C.M. 38723g; 22, x 15, U.C.M. 38723h.

28-32 - Holaspid cranidia. Notice the broad anterior border and the distinct paraglabellar tubercles on the sides of glabellar bases; 28, x 16, U.C.M. 38723n; 29, x 14, U.C.M. 38723o; 30, x 14, U.C.M. 38723p; 31, x 14, U.C.M. 38723q; 32, x 13, U.C.M. 38723.



Explanation of Plate 2

Figures 1-26 - Olenellus truemani Walcott

1-5 - Paraprotaspides. Notice the longitudinal fissure along the axis, and the pleural furrows on the fixigenae; 1-3, x 40, U.C.M. 38724a-c: 4, x 36, U.C.M. 38724d; 5, x 34, U.C.M. 38724e.

6-10 - Early meraspides, showing the disappearance of the longitudinal fissure, but distinct pleural furrows retained on the fixigenae; 6, a less complete shield, x 28, U.C.M. 38724f; 7, a well-preserved shield, x 30, U.C.M. 38724g; 8,9,10, three less well preserved shields; 8, x 30, U.C.M. 38724h; 9, x 24, U.C.M. 38724i; 10, x 20, U.C.M. 38724j.

20 - An early meraspid hypostoma, showing the spinose posterior margin, x 9.5, U.C.M. 38724t.

23 - A broken cephalon, showing a long, left metagenal spine, x 25, U.C.M. 38724w.

11-14 - Late meraspides, showing the disappearance of the pleural furrows and the presence of the fixigenal spines; 11, x 17, U.C.M. 38724k; 12, x 14, U.C.M. 38724ln; 13, x 16, U.C.M. 38724m.

21 - Hypostoma with shorter marginal spines and expanded median body, x 3, U.C.M. 38724u.

15-19 - Holaspides. 15, x 9, U.C.M. 38724o; 16, x 8, U.C.M. 38724p; 17, x 6.4, U.C.M. 38724q; 18,19, x 6, U.C.M. 38724.

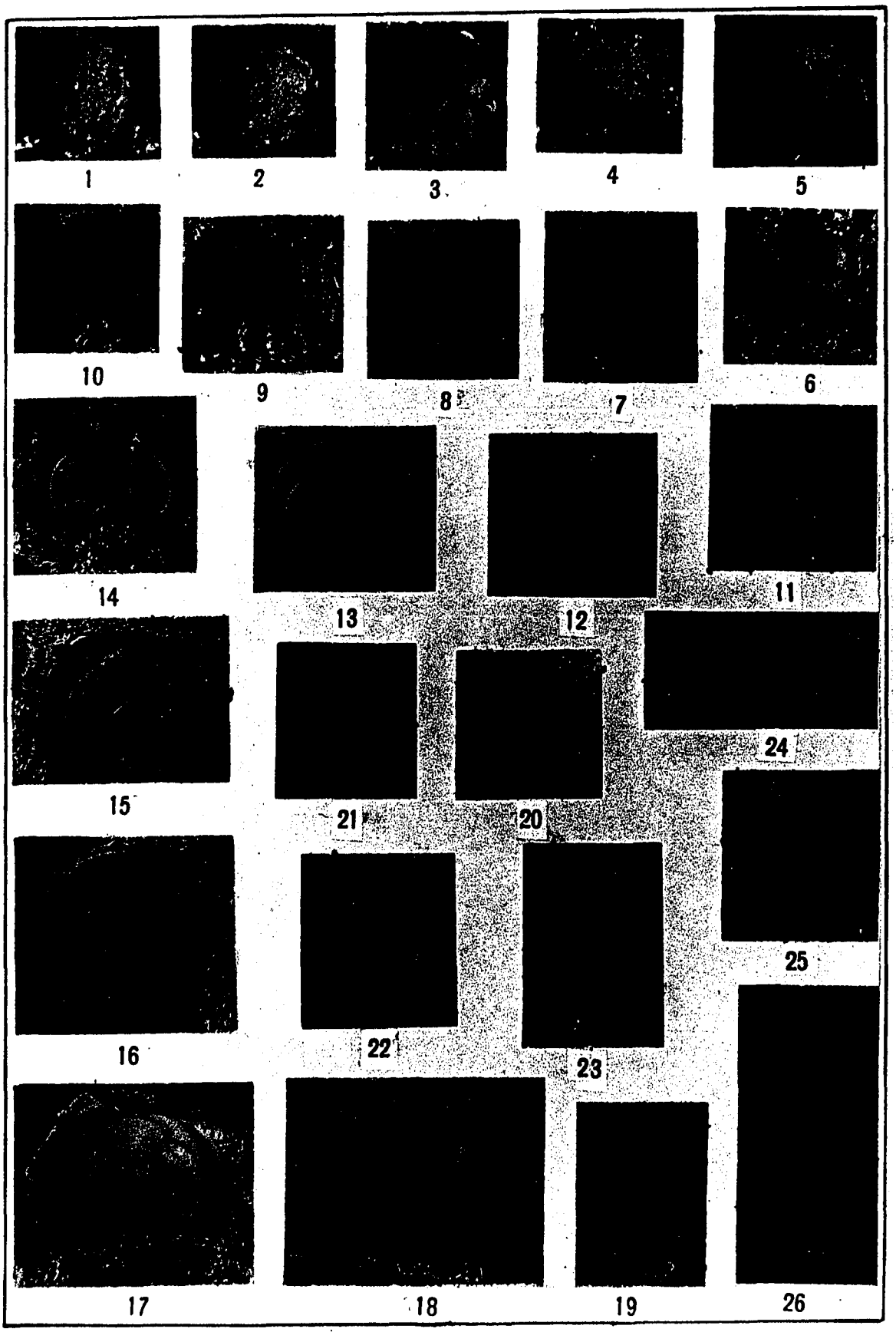
22 - Hypostoma, notice the expanded median body, x 3, U.C.M.

38724v.

24 - Part of the thoracic segment, showing the dorsal skeletal surface, x 10, U.C.M. 38724z.

25 - Part of the anterior glabella, showing shrunken surface; x 10, U.C.M. 38724x.

26 - Part of the cephalic marginal border, showing the pitted inner marginal furrow, x 1, U.C.M. 38724y.



Explanation of Plate 3

Figures 1-19 - Apomodocia conica, n. gen. et sp.

1 - Anaprotaspis, showing a longitudinal fissure along the axis, x 43, U.C.M. 38725a.

2,3 - Metaprotaspides, showing the differentiation of the axial and pleural lobes; 2, x 45, U.C.M. 38725b; 3, x 38, U.C.M. 38725c.

4-8 - Paraportaspides. Notice the segmentation of the protopygidium; 4,5, x 36, U.C.M. 38725d, e; 6, x 37, U.C.M. 38725f; 7, x 35, U.C.M. 38725g; 8, a cranidium without protopygidium, x 35, U.C.M. 38725h.

9-10 - Early meraspides. Notice that the cranidia bear no occipital spines, differing in this respect from Cedarina cordillerae; 9, x 40, U.C.M. 38725i; 10, x 31, U.C.M. 38725j.

11 - A late meraspis, showing the well developed preglabellar field and anterior border, x 17, U.C.M. 38725k.

12-19 - Holaspides. 12, x 11, U.C.M. 38725l; 13, x 10, U.C.M. 38725m; 14, x 9, U.C.M. 38725n; 15,16, dorsal and lateral views of a rather well-preserved cranidium, x 5.4, U.C.M. 38725; 18, a broken librigena, x 4.3, U.C.M. 38725o; 17,19, top and side views of a broken pygidium, x 3.6, U.C.M. 38725p.

Figures 20-31 - Laudonia canadiensis, n. sp.

20-21 - Two early meraspides. Notice the three pairs of marginal spines; 20, x 14, U.C.M. 38726a; 21, x 11, U.C.M. 38726b.

28,29 - Late meraspides. Notice the shortening of the anterior

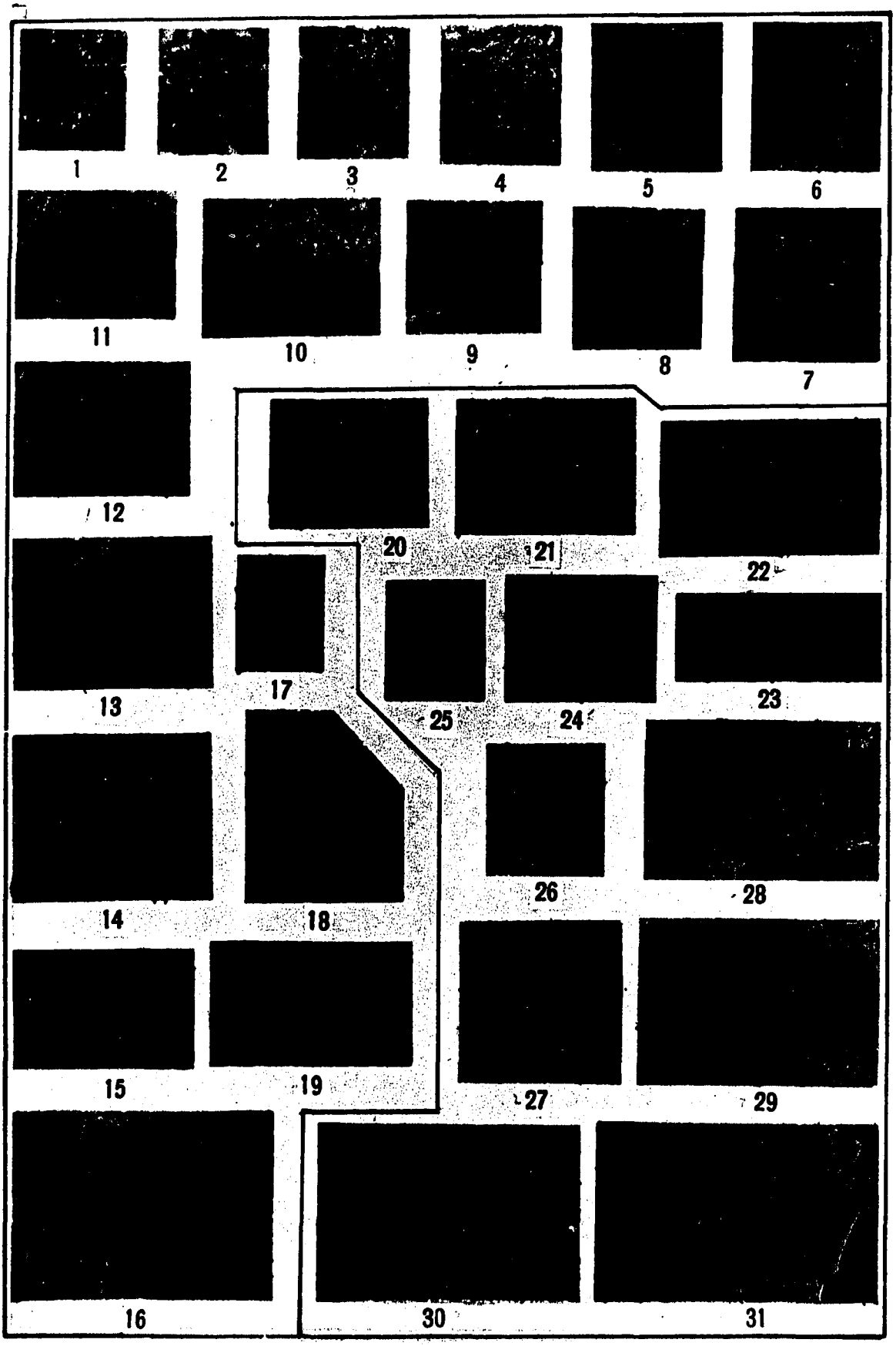
pair of marginal spines; 28, x 10.5, U.C.M. 38726g; 29, x 6.5, U.C.M. 38726h.

25 - Late meraspid hypostoma. Notice the long marginal spines, x 11, U.C.M. 38726d.

22-24,30,31 - Holaspides. Notice the disappearance of the anterior pair of marginal spines and the lengthening of the lateral genal spines; 22-24 dorsal, frontal, and lateral views of an incomplete cranidium, x 4.3, U.C.M. 38726c; 30, x 6.3, U.C.M. 38726i; 31, x 4.6, U.C.M. 38726.

26 - A broken holaspid hypostoma with shorter posterior marginal spines and expanded median body, x 2.5, U.C.M. 38726e.

27 - Part of the thoracic segment showing the serration along the anterior lateral margin, x 3.3, U.C.M. 38726f.



Explanation of Plate 4

Figures 1-23 - Ptarmigania aurita Resser

1-5 - Anaprotaspides. 1,2, showing the very faint axis; 1, x 40, U.C.M. 38727a; 2, x 43, U.C.M. 38727b; 3, showing the narrow depression along the axis, x 43, U.C.M. 38727c; 4,5, showing the slightly elevated axis; notice the posterior marginal median tubercle; 4, x 43, U.C.M. 38727d; 5, x 38, U.C.M. 38727e.

6,7 - Metaprotaspides. Notice the narrow axis and the distinct dorsal furrow; 6, x 40, U.C.M. 38727f; 7, x 38, U.C.M. 38727g.

8-13,15 - Paraprotaspides. Notice the glabella expanded both anterior and posteriorly; 8, x 37, U.C.M. 38727h; 9, x 37, U.C.M. 38727i; 10, x 35, U.C.M. 38727j; 11, x 33, U.C.M. 38727k; 12, x 37, U.C.M. 387271; 13, x 30, U.C.M. 38727m; 15, x 36, U.C.M. 38727o.

14,16-18 - Early meraspides, showing the glabella tapering posteriorly; 14, x 28, U.C.M. 38727n; 16, x 18, U.C.M. 38727p; 17, x 27, U.C.M. 38727q; 18, x 30, U.C.M. 38727r.

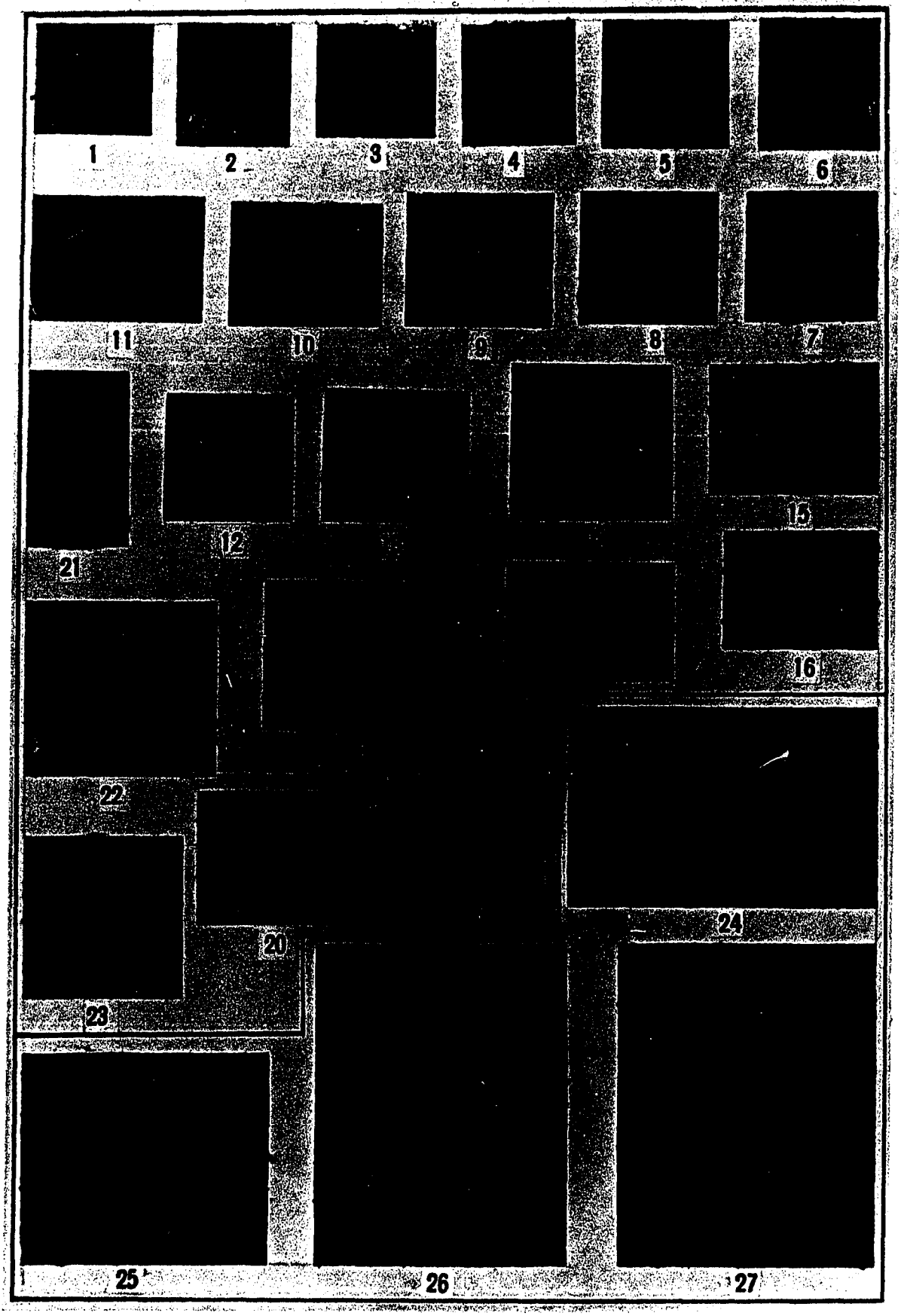
19,20 - Late meraspides. Notice the presence of the anterior border; 19, x 27, U.C.M. 38727s; 20, x 25, U.C.M. 38727t.

21-23 - Holaspides. 21,22, top and side views of a complete cranidium; 21,22, x 12, U.C.M. 38727; 23, x 17, U.C.M. 38727u.

Figures 24-27 - Acidaspis cincinnatiensis Meek

An isolated specimen showing two individuals facing each other,

cephalon directed to cephalon, and pygidium to pygidium. 24, lateral view, notice the upper and lower individuals; 25,27, cephalic and dorsal views of the smaller individual (upper one in fig. 24); 26, dorsal view of the larger individual, the cephalon and part of pleural lobe are broken off. All x 2.3, U.C.M. 38729.



Explanation of Plate 5

Figures 1-30 - Glyphaspis cf. parkensis Rasetti

1-3 - Anaprotaspides. Notice that the smallest instar shows a very faint fissure along the axis; 1, x 53, U.C.M. 38728a. 2, x 60, U.C.M. 38728b; 3, x 53, U.C.M. 38728c.

4,5 - Metaprotaspides, showing the differentiation of the axial and pleural lobes; 4, x 45, U.C.M. 38728d; 5, x 45, U.C.M. 38728e.

6,7 - Paraprotaspides, showing the presence of the protopygidium; 6, x 40, U.C.M. 38728f; 7, x 29, U.C.M. 38728g.

8-11 - Early meraspides, showing the development of the anterior border and the posterior migration of the palpebral lobes; 8, x 27, U.C.M. 38728h; 9, x 25, U.C.M. 38728i; 10, x 24, U.C.M. 38738j; 11, x 25, U.C.M. 38728k.

23,24 - Early meraspid pygidia, in each articulated series with three or four thoracic segments; 23, x 26, U.C.M. 38728t; 24, x 21, U.C.M. 38728u.

12-14 - Late meraspid cranidia. Notice the widening of the anterior brim and the truncate-conical glabella; 12, x 20, U.C.M. 38728l; 13, x 16, U.C.M. 38728m; 14, x 10 U.C.M. 38728n.

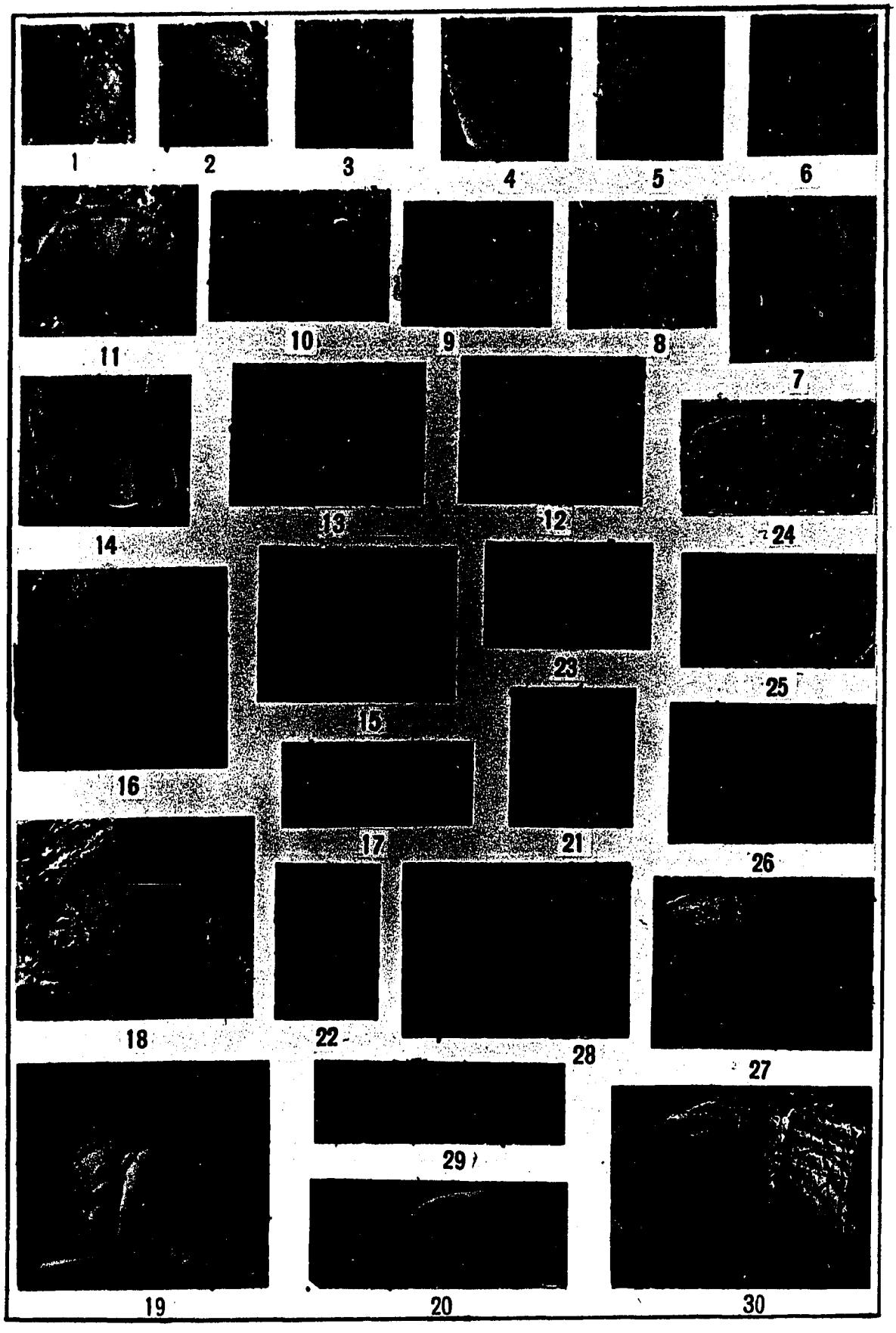
25 - A late meraspid pygidium, x 12, U.C.M. 38728v.

15-18,22,27 - Holaspides ("male"). 15, x 7.6, U.C.M. 38728o; 16, x 16, U.C.M. 38728p; 17,18, top and lateral views of a cranidium, notice the strongly upturned anterior brim, x 1.6,

U.C.M. 38728q; 22, a small, broken librigena, x 10, U.C.M. 38728s; 27, an elongate pygidium, x 1.7, U.C.M. 38728y.

19,20,26,28-30 - Holaspides ("female"). 19,20, dorsal and side views of a larger cranidium, showing the less upturned anterior brim, x 7, U.C.M. 38728; 26,28, two incomplete pygidia, showing the rounded outline; 26, x 1.7, U.C.M. 38728w; 28, x 1.9, U.C.M. 38728x; 29,30, dorsal and back views of a large pygidium, x 2, U.C.M. 38728z.

21 - An incomplete hypostoma, x 5.6, U.C.M. 38728r.



Explanation of Plate 6

Figures 1-14 - Kepisis stenotoides (Metthew), n. gen.

1,2,10,11 - Early meraspides. 1,2, two cranidia showing the longer anterior median spines and the slender glabellar, x 17, U.C.M. 38730a, b; 10,11, two pygidia with slender axis and spinose margins, x 25, U.C.M. 38730i, j.

3-5,12,13 - Late meraspides. 3-5, three cranidia with narrow and well developed preglabellar field and fine palpebral ridges; 3, x 11, U.C.M. 38730c; 4, x 14, U.C.M. 38730d; 5, x 13, U.C.M. 38730e; 12,13, two pygidia decorated with marginal spines; 12, x 16, U.C.M. 38730k; 13, x 15, U.C.M. 387301.

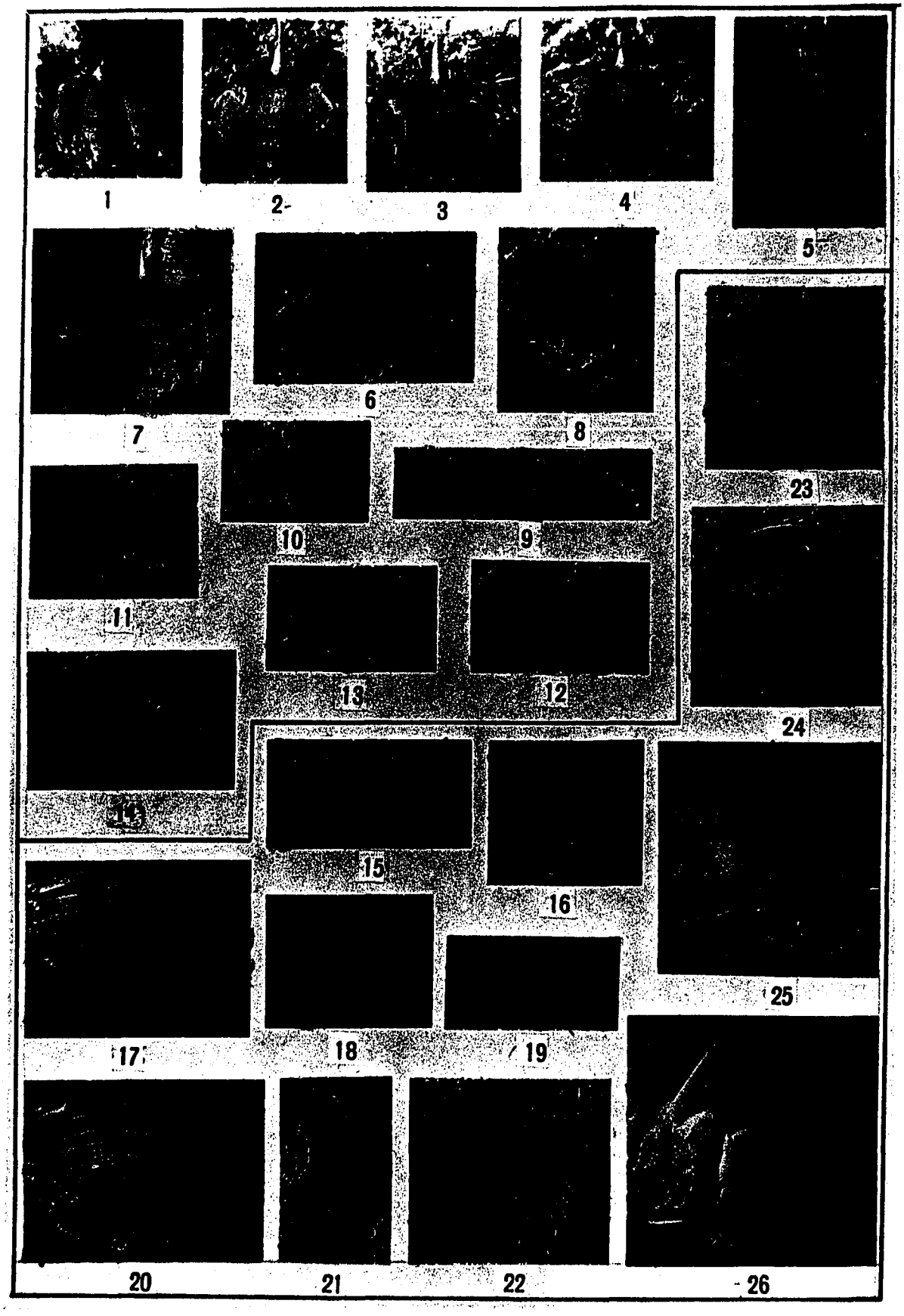
6-9,14 - Holaspides. 6, a less complete crandium, x 11, U.C.M. 38730f; 7, a rather complete crandium, x 5.5, U.C.M. 38730; 8, a small sized librigena, x 1.7, U.C.M. 38730g; 9, a broken thoracic segment, x 6.7, U.C.M. 38730h; 14, a rather well-preserved pygidium, x 11, U.C.M. 38730m.

Figures 15-26 - Iohomia sickia, n. gen. et sp.

15,18,19,21,22,25,26 - Holaspides ("male"). 15,26, frontal and dorsal views of an incomplete cranidium, x 2.5, U.C.M. 38737; 25, top view of an incomplete cranidium, showing the well impressed anterior median pit, x 2.5, U.C.M. 38737i; 18,19, top and back views of a pygidium, x 4.5, U.C.M. 38737c; 22, a broken pygidium, x 3.1, U.C.M. 38737f; 21, an imperfectly preserved librigena, x 5.4, U.C.M. 38737e.

16 - A meraspid cranidium, showing the large and scattered granules, x 10, U.C.M. 38737a.

17,20,23,24 - Holaspides ("female"). 17,20, two imperfectly preserved pygidia, showing the rounded outline; 17, x 2.2, U.C.M. 38737d; 20, x 1.8, U.C.M. 38737b; 23,24, two cranidia showing the narrower anterior border; 23, x 4.3, U.C.M. 38737g; 24, x 3, U.C.M. 38737h.



Explanation of Plate 7

Figures 1-29 - Cedarina cordillerae (Howell and Duncan)

1 - Anaprotaspis, x 52, U.C.M. 38731a.

2-4 - Metaprotaspides, showing the well developed axial and pleural lobes; 2, x 50, U.C.M. 38731b; 3, x 40, U.C.M. 38731c; 4, x 43, U.C.M. 38731d.

5-8 - Paraprotaspides, showing the well preserved dorsal furrow and protopygidium, but no distinct glabellar ring; 5, x 42, U.C.M. 38731e; 6, x 42, U.C.M. 38731f; 7, x 35, U.C.M. 38731g; 8, x 36, U.C.M. 38731h.

9,10,26 - Early meraspides, showing the development of the anterior borders; 9, x 28, U.C.M. 39731i; 10, x 24, U.C.M. 38731j; 26, a pygidium in articulated series with a or 4 thoracic segments, x 26, U.C.M. 38731y.

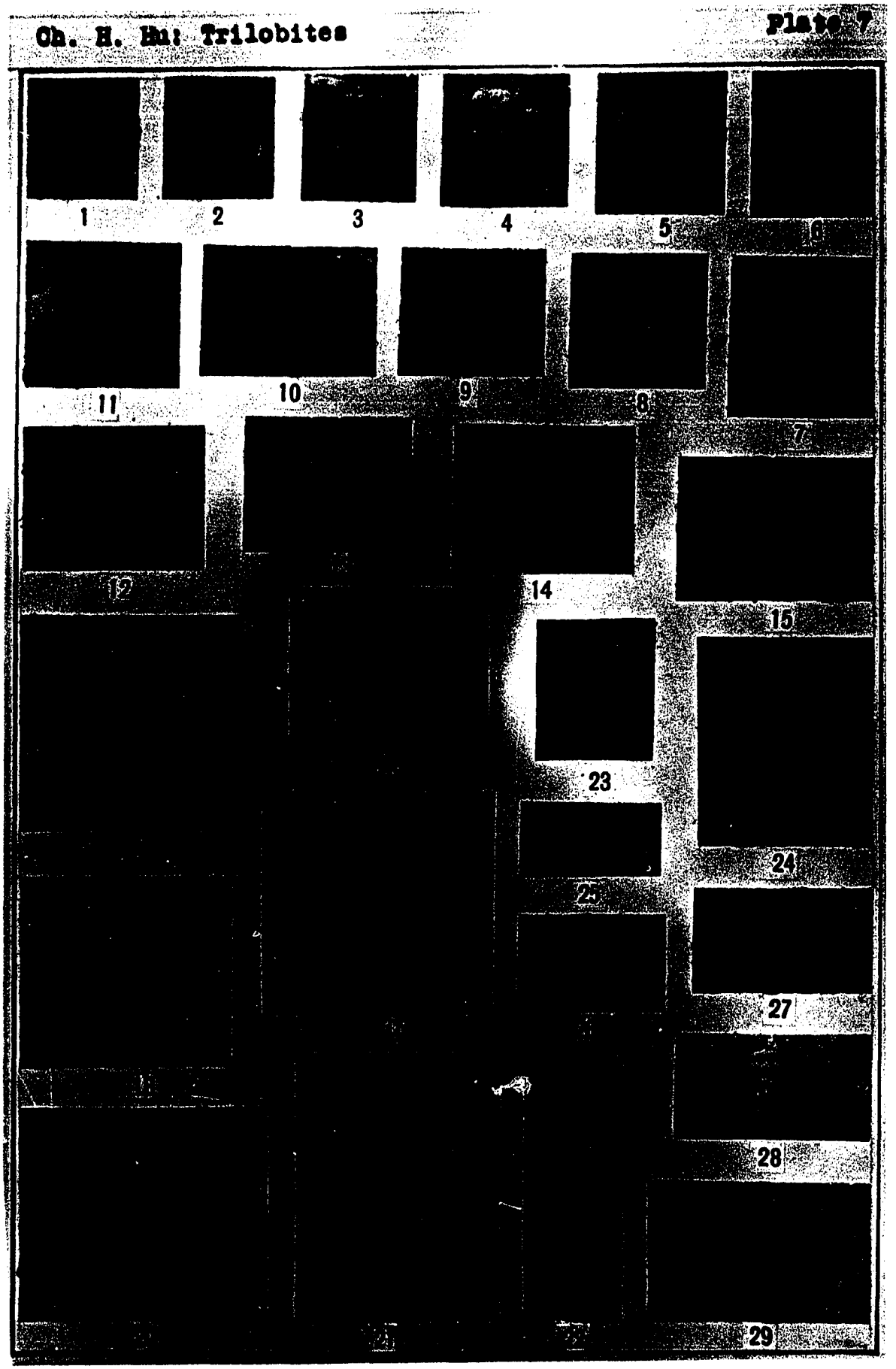
11-13,25 - Late meraspides. Notice the occipital spines; 11, x 23, U.C.M. 38731k; 12, x 19, U.C.M. 387311; 13, x 14, U.C.M. 38731m; 25, a pygidium possibly associated with one or two thoracic segments, x 8.3, U.C.M. 38731x.

14,15,17,18,20 - Holaspides ("female"). Notice the longer and narrower glabella; 14, x 9.5, U.C.M. 38731n; 15, x 9.5, U.C.M. 38731o; 17, x 6.2, U.C.M. 38731q; 18, x 4.5, U.C.M. 38731r; 20, x 4.7, U.C.M. 38731t.

16,19,21,22 - Holaspides ("male"), showing the wider and shorter glabella; 16, x 5.6, U.C.M. 38731p; 19, x 4.2, U.C.M. 38731s. 21,22, dorsal and side views of an incomplete cranidium,

x 3.7, U.C.M. 38731u.

23,24,27-29 - Holaspides. 23, an isolated hypostoma, x 8, U.C.M. 38731v; 24, a librigena, x 2.4, U.C.M. 38731w; 27-29, one small and two large pygidia; 27, x 11, U.C.M. 38731z; 28, x 6.5, U.C.M. 38731a'; 29, x 6.4, U.C.M. 38731b'.



Explanation of Plate 8

Figures 1-29 - Crepicephalus deadwoodiensis, n. sp.

1,2 - Anaprotaspides. 1, smallest shield size, showing no axial lobe or dorsal furrow, x 65, U.C.M. 38732a; 2, the shield shows a narrow depression along the anterior axis and a tubercle on the posterior end, x 68, U.C.M. 38732b.

3-7 - Metaprotaspides, showing the well differentiated axial and pleural lboes; 3, x 63, U.C.M. 38732c; 4, x 63, U.C.M. 38732d; 5, x 63, U.C.M. 38732e; 6, x 68, U.C.M. 38732f; 7, x 55, U.C.M. 38732g.

8-10 - Paraprotaspides, notice the indistinct protopygidium; 8, x 49, U.C.M. 38732h; 9, x 40, U.C.M. 38732i; 10, x 33, U.C.M. 38732j.

11-13 - Early meraspides, showing the well differentiated pygidia and the large granules on the fixigenae; 11, x 21, U.C.M. 38732k; 12, x 20, U.C.M. 387321; 13, x 19, U.C.M. 38732m.

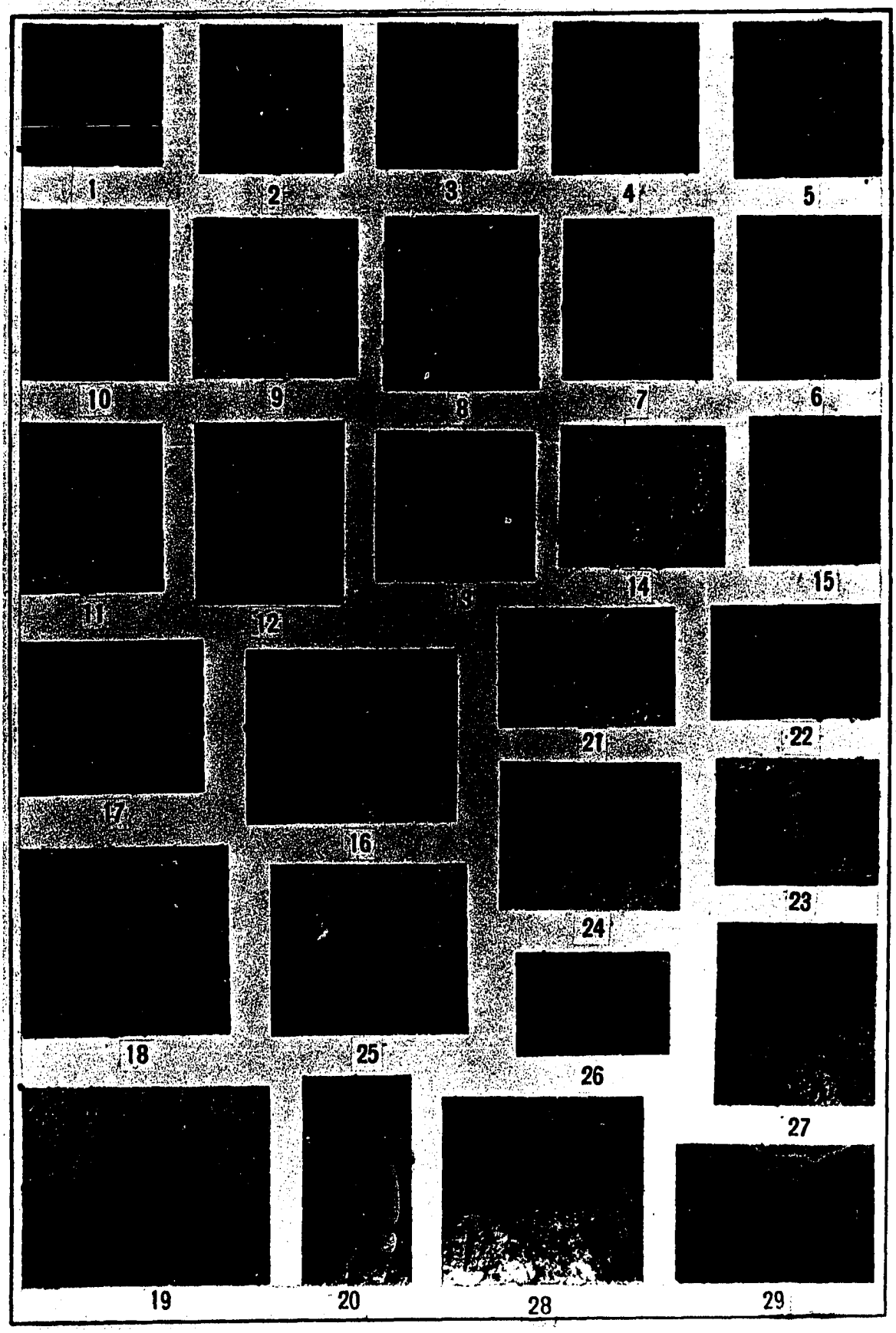
21 - Early meraspid pygidium. Notice the associated one or two thoracic segments, x 27, U.C.M. 38732r.

14-17 - Late meraspides. Notice the disappearance of the coarse granules; 14, x 16, U.C.M. 38732o; 16, x 16, U.C.M. 38732n. 16, x 15, U.C.M. 38732p; 17, x 12, U.C.M. 38732q.

22,23 - Two meraspides. Pygidia articulated with four thoracic segments; 22, x 30, U.C.M. 38732s; 23, x 16, U.C.M. 38732t.

18-20,24-29 - Holaspides. 18, a broken cranidium, x 14, U.C.M.

38732z; 19,20, top and side views of a cranidium, x 5.7, U.C.M. 38732; 24,28, two pygidia both associated with part of the thoracic segments; 24, x 13, U.C.M. 38732u; 28, x 12, U.C.M. 38732w; 25, ventral view of a pygidium. Notice the wrinkled doublure, x 10, U.C.M. 38732v; 27, a small librigena, x 17, U.C.M. 38732y; 26,29, dorsal and side views of a broken pygidium, x 5.1, U.C.M. 38732x.



Explanation of Plate 9

Figures 1-40 - Dunderbergia ? anyta (Hall and Whitfield)

1 - Anaprotaspis. A small shield shows the axial lobe with two pairs of central nodes and a longitudinal fissure, x 58, U.C.M. 38733a.

2-5 - Metaprotaspides. 2,3, dorsal and ventral views of an incomplete shield. Notice the three pairs of marginal spines and the perrostro-hypostoma, x 50, U.C.M. 38733b; 4,5, dorsal views of two shields. Notice the appearance of three pairs of central nodes; 4, x 53, U.C.M. 38733c; 5, x 55, U.C.M. 38733d.

6 - Ventral view of an incomplete shield, showing the perrostro-hypostoma slightly displaced, x 55, U.C.M. 38733e.

7-12 - Paraprotaspides, showing the fusion of the central nodes and the appearance of the protopygidium; 7, x 48, U.C.M. 38733f; 8, x 48, U.C.M. 38733g; 9, x 45, U.C.M. 38733h; 10,11, ventral and dorsal views of a shield, notice the librigenae in place, x 42, U.C.M. 38733i; 12, a complete shield, x 40, U.C.M. 38733j.

13,14,27,28,33 - Early meraspides. 13,14, dorsal views of two well preserved cranidia, showing the presence of the anterior borders; 13, x 25, U.C.M. 38733k; 14, x 20, U.C.M. 387331; 27, librigena showing the narrower ocular platform, x 16, U.C.M. 38733y; 28, hypostoma, showing the shorter marginal spine, x 46, U.C.M. 38733z; 33, a pygidium with spinose

marginal border and in articulated series with a or 4 thoracic segments, x 24, U.C.M. 38733e'.

15-17,26,29,34,35,37 - Late meraspides. 15-17, three complete cranidia showing the narrow preglabellar fields; 15, x 15, U.C.M. 38733m; 16, x 14, U.C.M. 38733n; 17, x 12, U.C.M. 38733o; 26, a librigena with wider ocular platform, x 8.2, U.C.M. 38733x; 29, a broken hypostoma showing the expansion of the median body and shorter posterior marginal spines, x 37, U.C.M. 38733a'; 34,35,37, three pygidia each in articulated series with one or two thoracic segments, notice the disappearance of the marginal spines and the presence of a median notch on the posterior margin; 34, x 26, U.C.M. 38733f'; 35, x 26, U.C.M. 38733g'; 37, x 25, U.C.M. 38733i'.

23 - A well preserved rostral plate, x 8, U.C.M. 38733u.

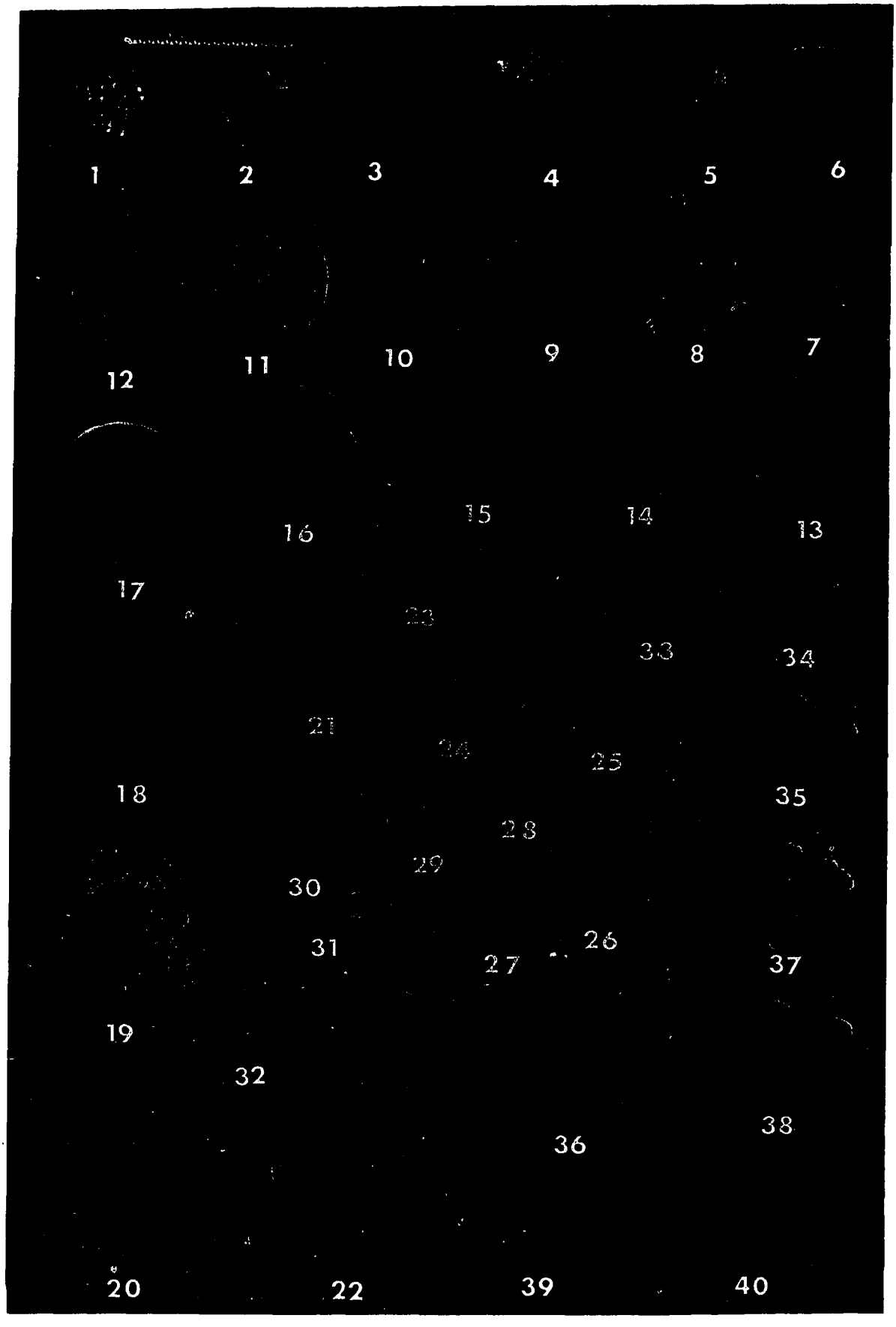
19,20,21,25,36,39 - Holaspides ("female"). 19, x 6.5, U.C.M. 38733p; 20, x 3.8, U.C.M. 38733; 21, x 9, U.C.M. 38733r; 25, x 3.5, U.C.M. 38733w; 36, x 14, U.C.M. 38733h'; 39, x 18, U.C.M. 38733k'.

18,22,24,38,40 - Holaspides ("male"). 18, x 6.8, U.C.M. 38733o; 22, x 4.4, U.C.M. 38733t; 24, x 3.8, U.C.M. 38733v; 38, x 16, U.C.M. 38733j; 40, x 4, U.C.M. 38733l'.

30 - A larger hypostoma, showing the more prominent median body and the absence of marginal spines, x 9.5, U.C.M. 38733b'.

31 - A broken thoracic segment showing the long right pleural spine, x 4, U.C.M. 38733c'.

32 - A pair of thoracic segments with the shorter pleural spines, x 29, U.C.M. 38733d'.



Explanation of Plate 10

Figures 1-36 - Dytremacephalus granulosus Palmer

1 - Anaprotaspis. An incomplete shield showing four axial rings, x 56, U.C.M. 38734a.

2-6 - Metaprotaspides. 2,3, dorsal and ventral views of a well preserved specimen; notice that the perrostro-hypostoma has a pair of large lateral spines, x 54, U.C.M. 38734b; 4,5, two shields showing the five axial rings and faint pleural furrows, x 57, U.C.M. 38734c; x 55, U.C.M. 38734d; 6, ventral view of an incomplete shield showing the slightly displaced hypostoma; notice the large lateral spines, x 58, U.C.M. 38734e.

7-14 - Paraprotaspides. 7, a well preserved shield, x 62, U.C.M. 38734f; 8,9, ventral and dorsal views of a complete shield, showing the perrostro-hypostoma slightly displaced, x 62, U.C.M. 38734g; 10,11, two broken shields, x 50, U.C.M. 38733h; x 52, U.C.M. 38734i; 12, a well preserved shield showing the protopygidia, x 40, U.C.M. 38734j; 13,14, two cranidia without protopygidia; 13, x 42, U.C.M. 38734k; 14, x 34, U.C.M. 38734l.

15-17,24,29-32 - Early meraspides. 15-17, three cranidia; notice the appearance of the anterior border; 15, x 32, U.C.M. 38734m; 16, x 25, U.C.M. 38734n; 17, x 21, U.C.M. 38734o; 24, a hypostoma, x 15, U.C.M. 38734u; 29, a librigena with narrower ocular platform and shorter genal spines, x 22,

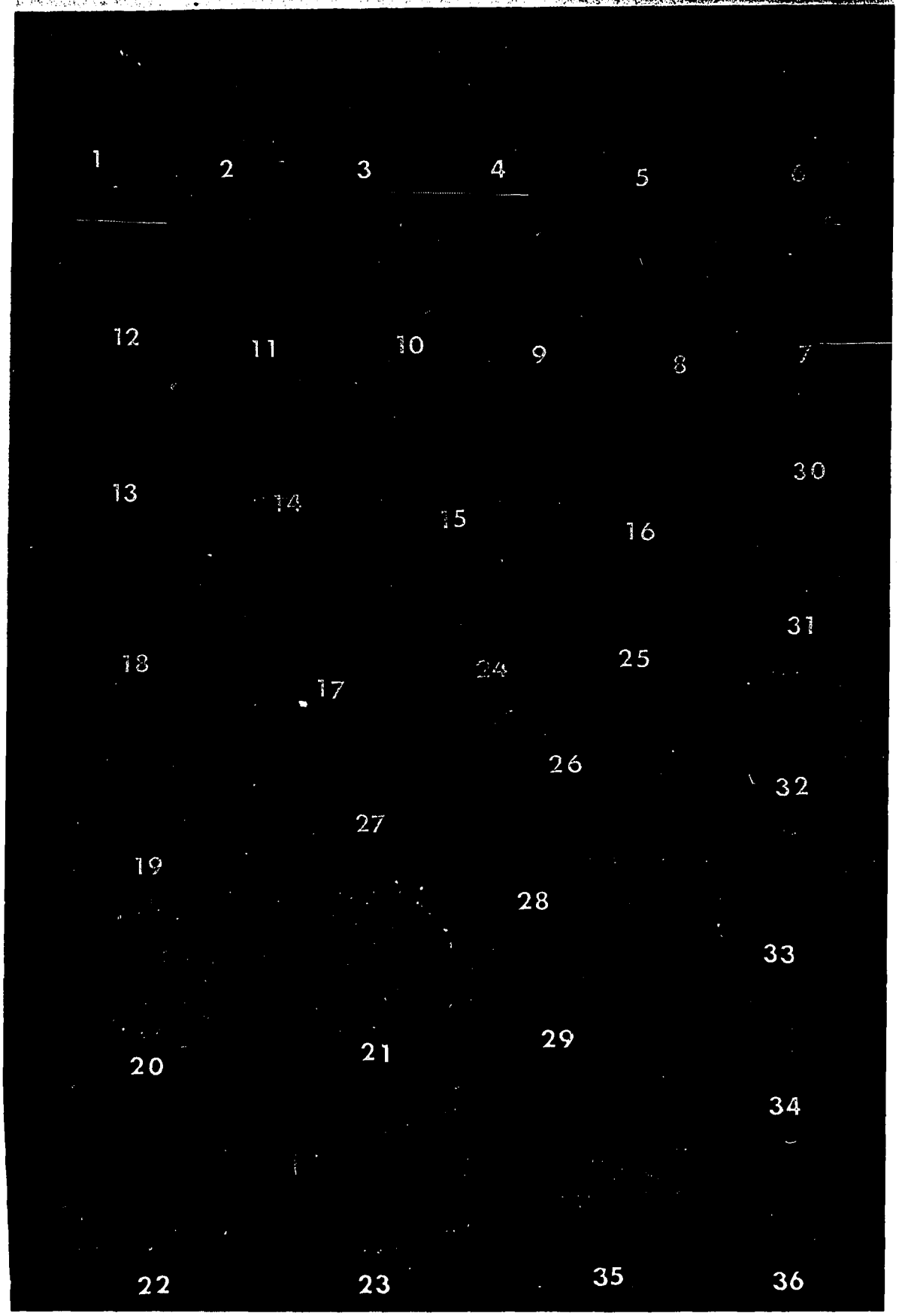
U.C.M. 38733a'; 30-32, three pygidia, each in articulated series with two or three thoracic segments; notice that the rather shorter marginal spines, and the axial ring tubercle, are different from those of Dunderbergia; 30, x 36, U.C.M. 38734b'; 31, x 31, U.C.M. 38734c'; 32, x 20, U.C.M. 38734d'.

18,19,33,34 - Late meraspides. 18,19, two cranidia with narrow preglabellar field; 18, x 15, U.C.M. 38734p; 19, x 16, U.C.M. 38734q; 33,34, two pygidia each associated with one or two thoracic segments; 33, x 34, U.C.M. 38734e'; 34, x 33, U.C.M. 38734f'.

21,23,28,35 - Holaspides ("male"). 21, x 15, U.C.M. 38734s; 23, x 10, U.C.M. 38734v; 28, x 9.4, U.C.M. 38734z; 35, x 13, U.C.M. 38734g'.

25,26 - Top and side views of two thoracic segments; 25, x 15, U.C.M. 38734w; 26, x 16, U.C.M. 38734x.

20,22,27,36 - Holaspides ("female"). 20, x 10, U.C.M. 38734r; 22, x 9, U.C.M. 38734t; 27, x 7.5, U.C.M. 38734y; 36, x 15, U.C.M. 38734h'.



Explanation of Plate 11

Figures 1-34 - Ptychaspis bullasus Lochman and Hu

1 - Metaprotaspis. Notice the three pairs of axial nodes and the longitudinal fissure along the axis, x 45, U.C.M. 38735a.

2-4 - Paraprotaspides. Notice the fusion of the axial nodes and the presence of the protopygidium; 2, x 46, U.C.M. 38735b; 3, x 35, U.C.M. 38735c; 4, x 29, U.C.M. 38738d.

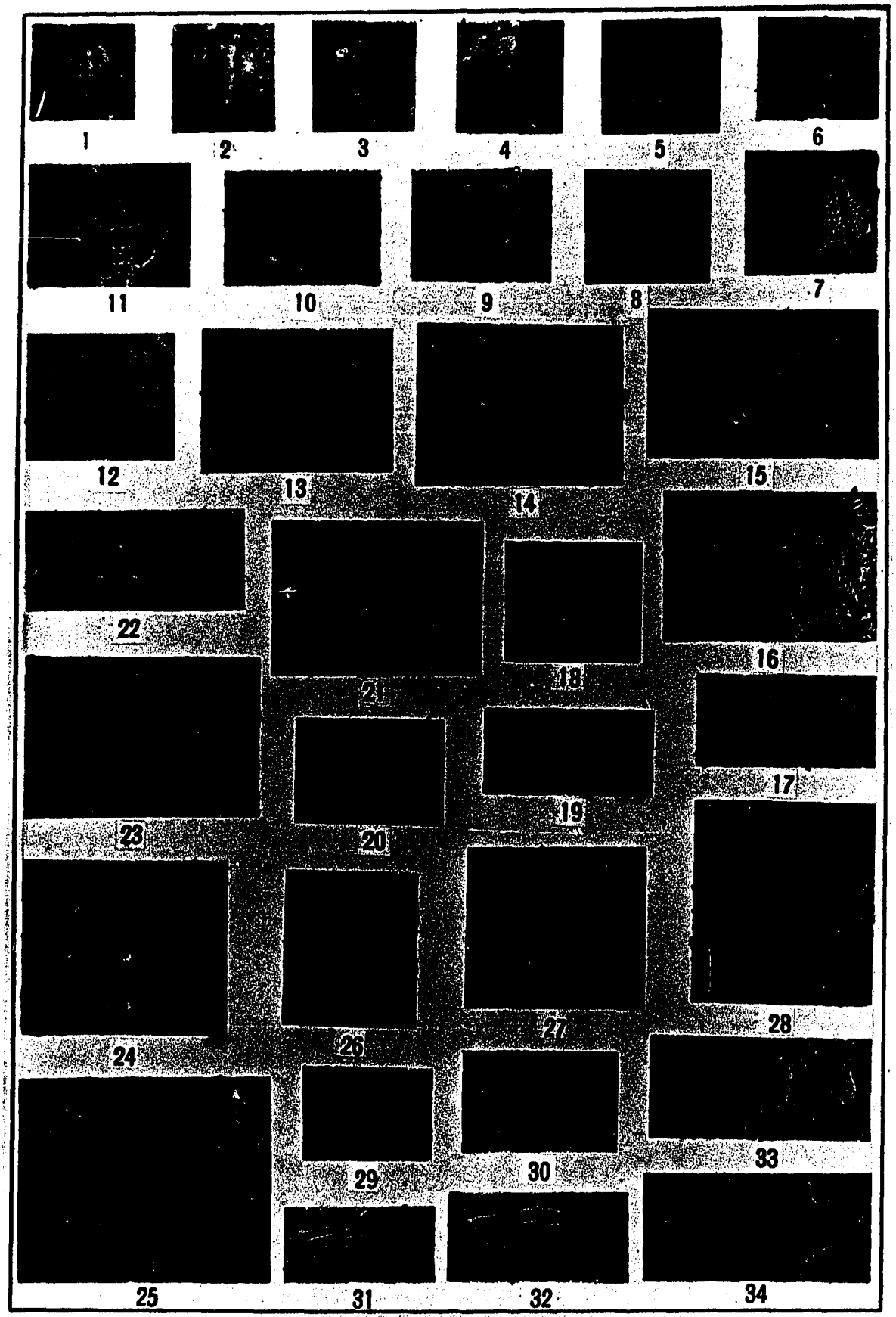
5-7 - Early meraspides. Notice the disappearance of the anterior pits and the conical shaped glabella; 5, x 20, U.S. N.M. 137100a; 6, x 15, U.C.M. 38735e; 7, x 13, U.C.M. 38735f.

29,30 - Two pygidia articulated with three or four thoracic setments; 29, x 14, U.C.M. 38735w; 30, x 16, U.C.M. 38735x.

8-13,26,27,31 - Late meraspides. 8-13, showing the broadly based glabella; 8-10, x 12, U.C.M. 38735g,h,i; 11, x 13, U.C.M. 38735k; 12, x 12, U.C.M. 38735j; 13, x 10, U.C.M. 387351; 26,27, Librigenae, showing the wider ocular platform; 26, x 6, U.C.M. 38735t; 27, x 5, U.C.M. 38735u; 31, late meraspid pygidium, x 7.5, U.C.M. 38735q.

14-25,28,32,33,34 - Holaspides; 15, x 8.6, U.C.M. 38735m; 16,17, dorsal and side views of a cranidium, x 6.2, U.C.M. 38735; 14,18,19, top and frontal views of a cranidium, x 5, U.C.M. 38735n; 20,21, x 10, U.C.M. 38735o; 22, x 6, U.C.M. 38735p; 23, x 4.4, U.C.M. 38735q; 24, x 3.3, U.C.M. 38735r; 25, x 2.7, U.C.M. 38735s; 28, a librigena, showing the narrower ocular platform, x 6.6, U.C.M. 38735v; 32-34, three

pygidia; x 8.5, U.C.M. 38735y; 32, x 2.8, U.C.M. 38735z; 34, x 3, U.S.N.M. 13700h.



Explanation of Plate 12

Figures 1-32 - Olenus gibbosus (Wahlenberg)

1-3 - Metaprotaspides. Notice the longitudinal fissure along the axis and the presence of ridges on the pleural lobes, x 55, U.C.M. 38736a-c.

4-8 - Paraprotaspides, showing the fusion of the axial nodes and the appearance of the protopygidium, 4, x 66, U.C.M. 38736d; 5, x 50, U.C.M. 38736e; 6, x 42, U.C.M. 38736f; 7, x 50, U.C.M. 38736g; 8, x 42, U.C.M. 38736h.

9-12 - Early meraspides, showing the development of the anterior border; 9, x 45, U.C.M. 38736i; 10, x 30, U.C.M. 38736j; 11, x 23, U.C.M. 38736k; 12, x 20, U.C.M. 387361.

29 - Early meraspid pygidium, x 27, U.C.M. 38736z.

13-18 - Late meraspides, showing the development of the preglabellar field and the impression of the glabellar furrows; 13, x 21, U.C.M. 38736m; 14, x 17, U.C.M. 38736n; 15, x 16, U.C.M. 38736o; 16, x 16, U.C.M. 38736p; 17, x 14, U.C.M. 38736q; 18, x 14, U.C.M. 38736r.

25,26 - Late meraspid librigenae; 25, x 23, U.C.M. 38736v; 26, x 17, U.C.M. 38736w.

30 - Late meraspid pygidium, x 20, U.C.M. 38736a'.

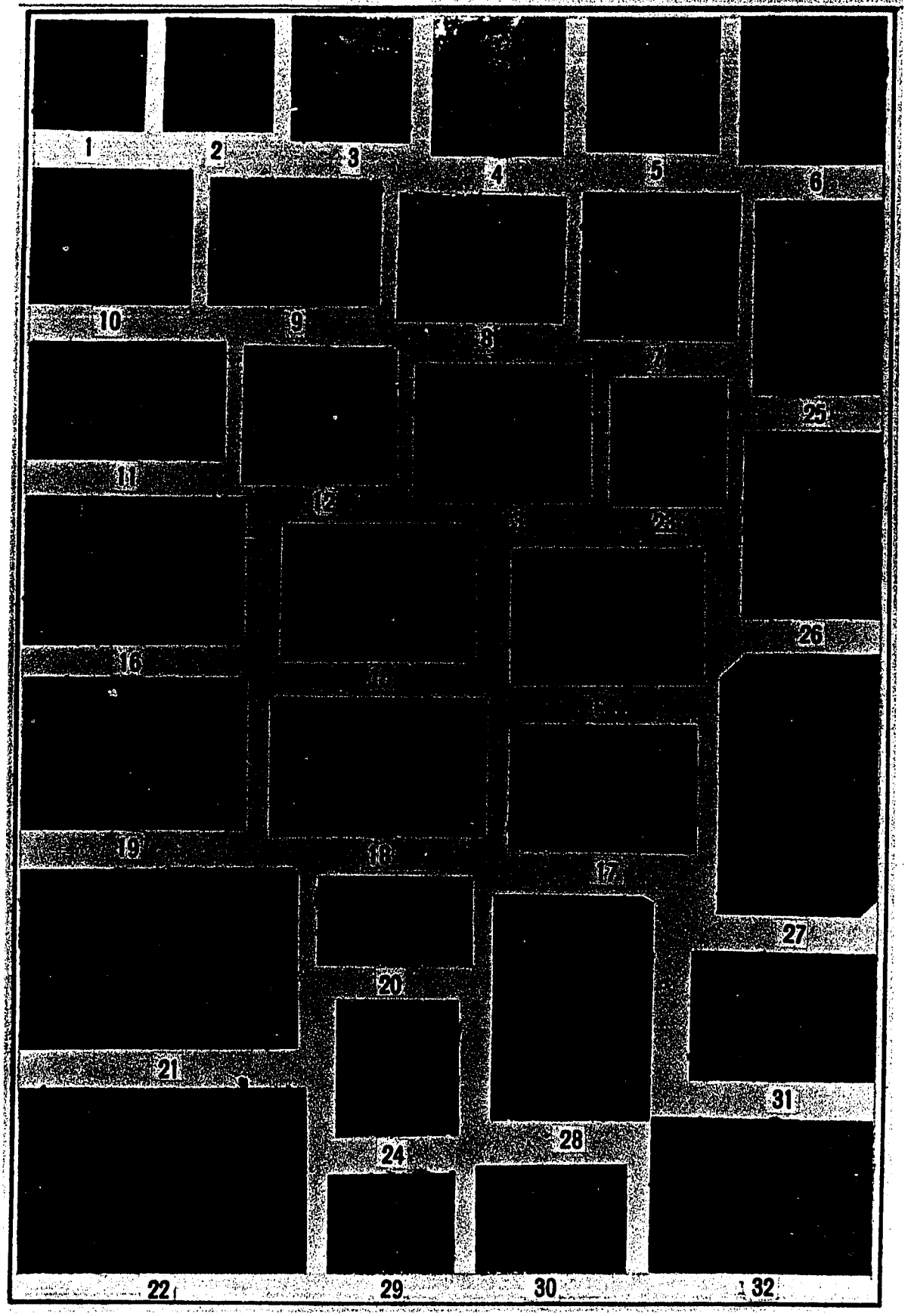
19-22 - Holaspid cranidia; 19, x 7.8, U.C.M. 38736s; 20, lateral view of a cranidia, x 4.6, U.C.M. 38736d'; 21, x 1.3, U.C.M. 38736e'; 22, x 4.5, U.C.M. 38736.

23,24 - Hypostomata. 23, x 23, U.C.M. 38736t; 24, x 20, U.C.M.

38736u.

27,28 - Two incomplete librigenae; 27, x 8, U.C.M. 38736x; 28, x 4.2, U.C.M. 38736y.

31,32 - Two pygidia, 31, x 9, U.C.M. 38736b'; 32, x 7, U.C.M. 38736c'.



Explanation of Plate 13

Figures 1-34 - *Acerocare ecorne* Angelin

1-2 - Metaprotaspides. Notice the two pairs of axial nodes and the indistinct fourth and fifth axial rings; 1, x 50, U.C.M. 38738a; 2, x 50, U.C.M. 38738b.

3-6 - Paraprotaspides, showing the distinct axial rings and steeply deflected protopygidium; 3,4, notice the pleural lobe furrows, x 56, U.C.M. 38738c; U.C.M. 38738d; 5, x 47, U.C.M. 38738e; 6, x 48, U.C.M. 38738f.

7-9 - Early meraspides, showing the expansion of posterior fixigenal borders; 7, x 35, U.C.M. 38738g; 8, x 32, U.C.M. 38738h; 9, x 25, U.C.M. 38738i.

26 - Early meraspid pygidium associated with one thoracic segment, x 22, U.C.M. 38738y.

10-12 - Late meraspides, showing the dorsal facial sutures and the posteriorly expanded glabella; 10, x 26, U.C.M. 38738h; 11, x 25, U.C.M. 38738j; 12, x 22, U.C.M. 38738k.

20 - Late meraspid librigena, x 11, U.C.M. 38738s.

22 - Late juvenile pygidium, notice the slender axis, x 18, U.C.M. 38738u.

27-29 - Three juvenile pygidia, 27, x 30, U.C.M. 38738z; 28, x 24, U.C.M. 38738a'; 29, x 19, U.C.M. 38738b'.

15,17,19,24,32,34 - Holaspides ("male"). 15, x 13, U.C.M. 38738n; 17, x 10, U.C.M. 38738p; 19, x 8, U.C.M. 38738r; 24, x 9.2, U.C.M. 38738w; 32, x 7.2, U.C.M. 38738e'; 34,

x 6.8, U.C.M. 38738g'.

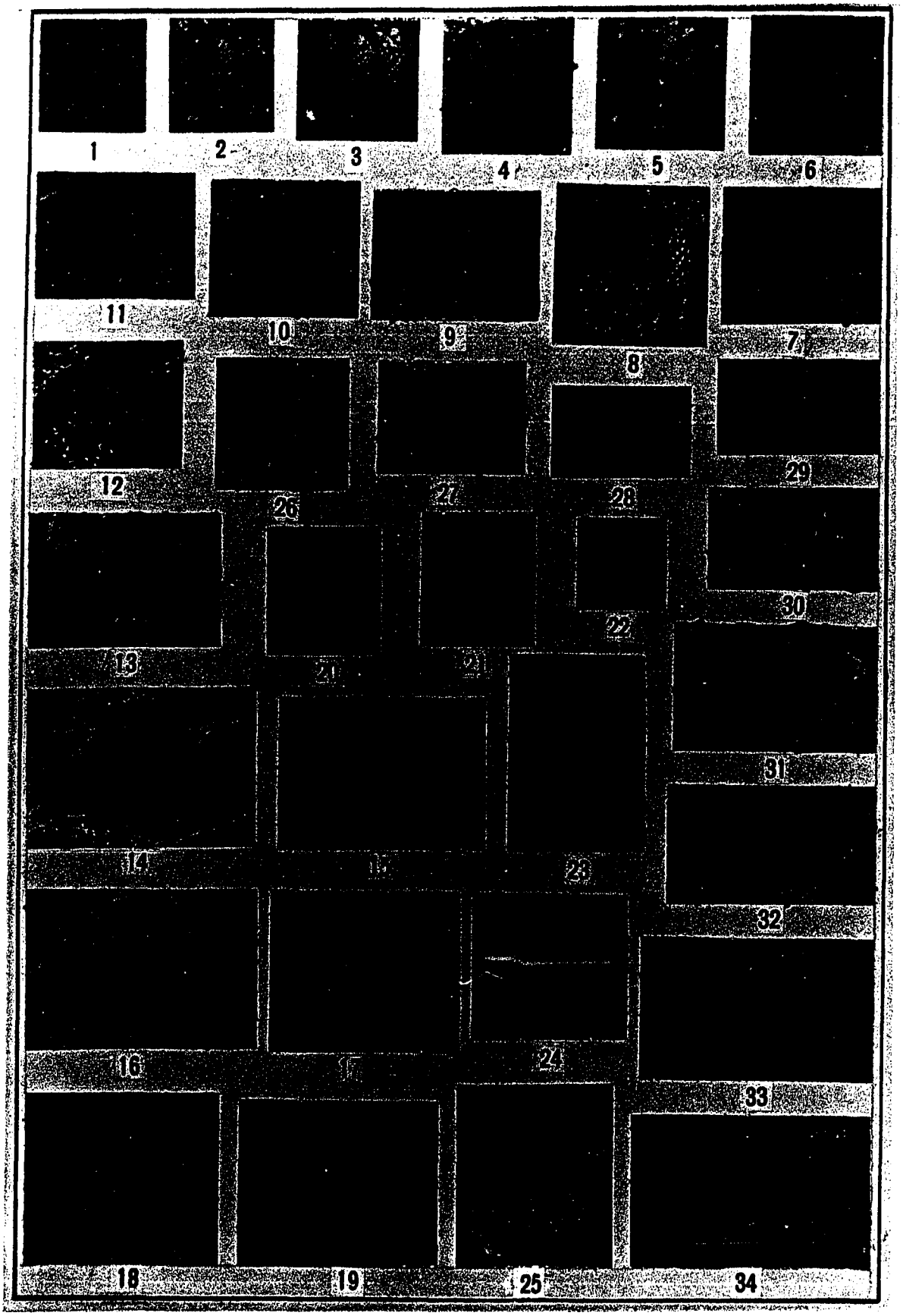
13,14,16,18 - Holaspid cranidia ("female"). Notice that the glabellae are narrower and longer than those of the "male" form; 13, x 16, U.C.M. 387381; 14, x 10, U.C.M. 38738m; 16, x 10, U.C.M. 38738o; 18, x 8, U.C.M. 38738q.

23 - Early holaspis, showing the cranidium associated with a few thoracic segments, x 9, U.C.M. 38738v.

25 - A "female" librigena; notice the narrower ocular platform, x 9, U.C.M. 38738x.

30,31,33 - Holaspid pygigidia ("female"). Notice that they are more rounded in comparison with the pygidia of the "male" form; 30, x 11, U.C.M. 38738c'; 31, x 8.4, U.C.M. 38738d'. 33, x 8.4, U.C.M. 38738f'.

21 - Hypostoma. Notice the expanded median body and the narrower posterior brim in comparison with figure 22, x 11, U.C.M. 38738t.



Explanation of Plate 14

Figures 1-28 - Missisquoia cyclochila, n. sp.

1 - Anaprotaspis. The left side of the shield missing; notice the axial lobe composed of a small frontal lobe, two pairs of axial nodes, and a large terminal lobe, x 70, U.C.M. 38749a.

2,3 - Metaprotaspides, showing the fusion of the axial nodes and the distinct axial rings; 2, x 70, U.C.M. 38749b; 3, x 70, U.C.M. 38749c.

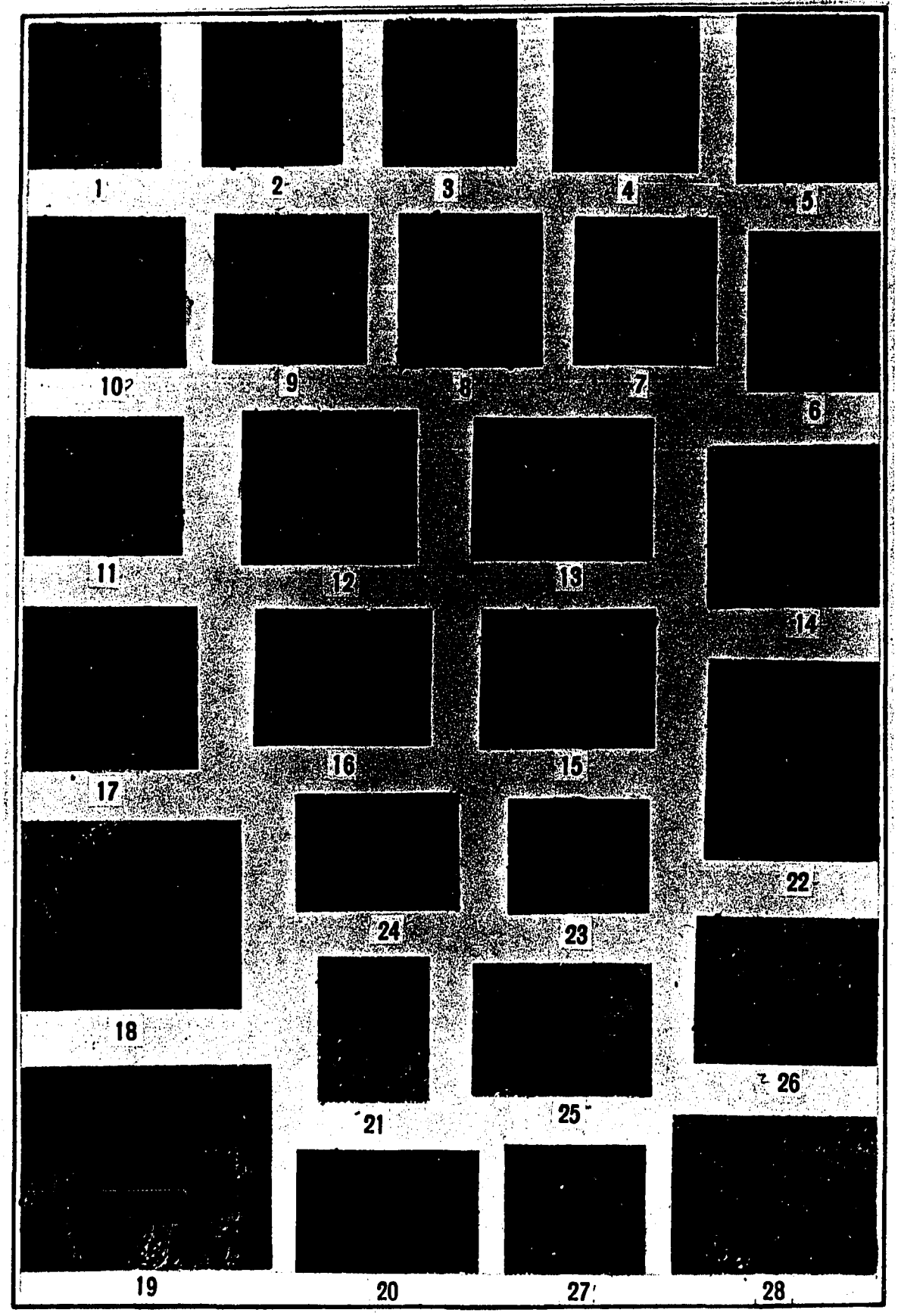
4-7 - Paraprotaspides. Notice the narrow, transverse protopygidium steeply deflected behind the posterior cranidial margin; 4, x 10, U.C.M. 38749d; 5, x 66, U.C.M. 38749e; 6, x U.C.M. 38749f; 7. x 57, U.C.M. 38749g.

8-15, 23 - Early meraspides. Notice the separation of the glabellar furrows; 8, x 50, U.C.M. 38749h; 9, x 48, U.C.M. 38749i; 10, x 47, U.C.M. 38749j; 11, x 43, U.C.M. 38749k; 12, x 45, U.C.M. 38749l; 13, x 45, U.C.M. 38749m; 14, x 40, U.C.M. 38749n; 15, x 30, U.C.M. 38749o; 23, roundly triangular pygidium in articulated series with possibly three thoracic segments, x 50, U.C.M. 38749u.

16,17,24,25 - Late meraspides. 16,17, two cranidia showing the appearance of the anterior border and shortening of the glabellar furrows, 16, x 24, U.C.M. 38749p; 17, x 20, U.C.M. 38749q; 24,25, two pygidia having the terminal portion extended to the posterior margin; 24, x 28, U.C.M. 38749v;

25, x 36, U.C.M. 38749x.

18-22,26-28 - Holaspides. 18, party exfoliated cranidium, x 18, U.C.M. 38749r; 19,20, dorsal and side views of a partly exfoliated cranidium, x 12, U.C.M. 38749; 21, incomplete hypostoma, x 18, U.C.M. 38749s; 22, broken librigena, x 20, U.C.M. 38749t; 26, less complete pygidium; notice that the axial lobe is not extended to the posterior margin, x 10, U.C.M. 38749x; 27,28, dorsal and side views of a complete pygidium, x 19, U.C.M. 38749y.



Explanation of Plate 15

Figures 1-26 - Highgatella facila, n. sp.

1-5 - Metaprotaspides. Notice the indistinct protopygidium at the posterior margin of the shield; 1-4, x 62, U.C.M. 38740a-d; 5, x 53, U.C.M. 38740e.

6 - Paraprotaspis, x 53, U.C.M. 38740f.

7-9 - Early meraspides. Notice the presence of the anterior borders; 7, x 40, U.C.M. 38740g; 8, x 38, U.C.M. 38740h; 9, x 40, U.C.M. 38740i.

10,11 - Late meraspides, showing the preglabellar fields; 10, x 30, U.C.M. 38740j; 11, x 25, U.C.M. 38740k.

13,14,17,20 - Holaspides ("male" form). Notice the shorter and broader glabellae; 13, x 11, U.C.M. 38740m; 14, x 14, U.C.M. 38740n; 17, x 10, U.C.M. 38740q; 20, x 6, U.C.M. 38740r.

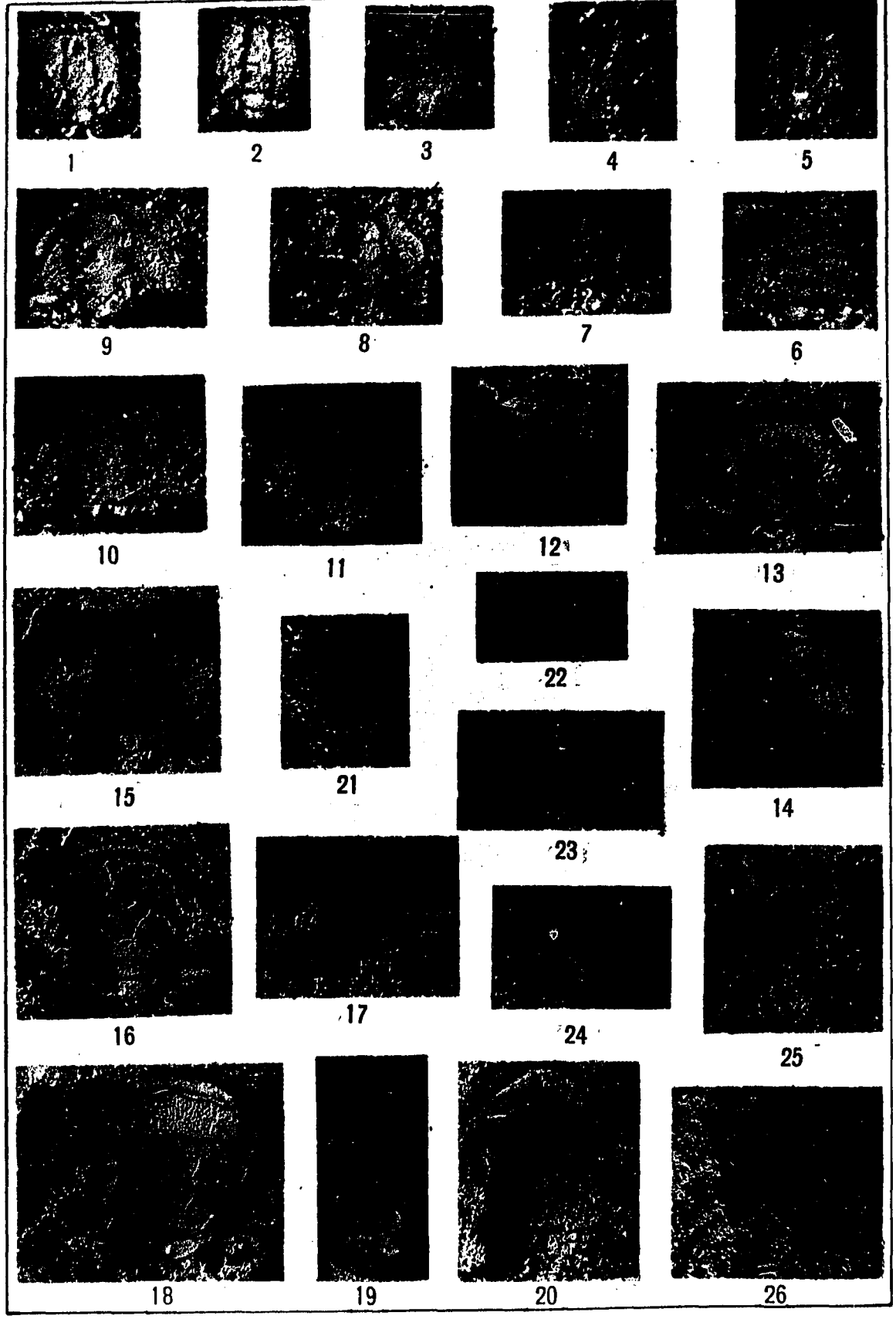
12,15,16,18,19 - Holaspides ("female"), showing the longer and shorter glabellae and slightly wider preglabellar field; 12, x 18, U.C.M. 387401; 15, x 8, U.C.M. 38740o; 16, x 15, 38740p; 18,19, top and side views of a less complete cranidium, x 6, U.C.M. 38740.

21 - A nearly complete hypostoma, x 24, U.C.M. 38740s.

22,24 - Two "female" pygidia; notice that each axial lobe is divided into two rings only; 22, x 30, U.C.M. 38740t; 24, x 12, U.C.M. 38740v.

23 - A "male" pygidium. Notice the axis is divided into three axial rings, x 25, U.C.M. 38740u.

25,26 - Two librigenae; 25, x 5, U.C.M. 38740w; 26, x 5, U.C.M. 38740x.



Explanation of Plate 16

Figures 1-39 - Libetella corona, n. gen. et sp.

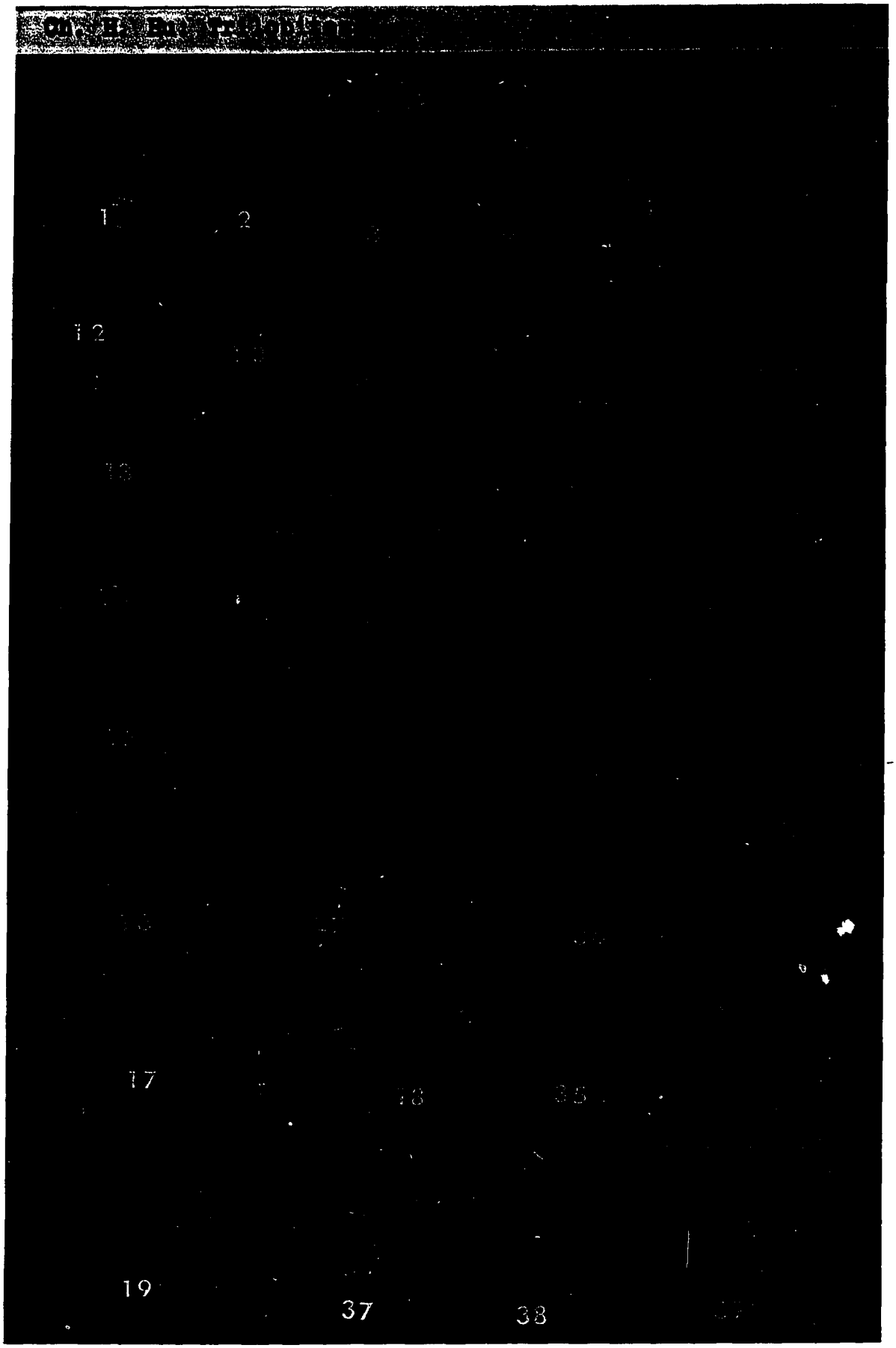
1-4,7,8 - Paraprotaspides. 1,2, dorsal and ventral views of a rather complete shield, x 38, U.C.M. 38741a; 3,4, two nearly complete shields, x 39, U.C.M. 38741b, c; 7,8, dorsal and ventral views of a slightly deformed shield, notice the librigena and hypostoma in place, x 35, U.C.M. 38741f.

5,6,9-11 - Early meraspides. Notice the migrations of the palpebral lobes during the growth periods; 5, x 30, U.C.M. 38741d; 6, x 29, U.C.M. 38741e; 9, x 26, U.C.M. 38741g; 10, x 25, U.C.M. 38741h; 11, x 26, U.C.M. 38741i.

12-16,25,26,28-31 - Late meraspides. 12-16 showing the development of the posterior fixigenal borders and the lateral widening of the glabellae; 12, x 22, U.C.M. 38741j; 13, x 18, U.C.M. 38741k; 14, x 16, U.C.M. 38741l; 15, x 18, U.C.M. 38741m; 16, x 15, U.C.M. 38741n; 25,26, ventral and dorsal views of a hypostoma; notice three pairs of posterior marginal spines, x 10, U.C.M. 38741w; 28-31, dorsal, posterior, and horizontal views of four pygidia; notice the different directions of the marginal spines; 28,29, x 20, U.C.M. 38741x; 30, x 21, U.C.M. 38741y; 31, x 36, U.C.M. 38741z.

17-27,32-39 - Holaspides. 17-19, three cranidia; 17, x 15, U.C.M. 38741o; 18, x 11, U.C.M. 38741p; 19, x 9.4, U.C.M. 38741q; 20-22, top and lateral views of three librigenae, showing the marginal spines and the stolked eyes, x 20,

U.C.M. 38741r; 21, x 21, U.C.M. 38741s; 22, x 15, U.C.M. 38741t; 23, a pair of thoracic segments, x 8.2, U.C.M. 38741u; 24,27, ventral and dorsal views of a hypostoma, x 10, U.C.M. 38741v; 32,34, top and ventral views of a pygidium, x 22, U.C.M. 38741a'; 33,35, two pygidia; 33, x 28, U.C.M. 38741b'; 35, x 14, U.C.M. 38741c'; 36,39, ventral and dorsal views of a less complete skelton in fig. 36, (the thoracic segments and pygidium were broken off by an accident after fig. 39 was taken), x 13, U.C.M. 38741d'; 37,38, ventral and dorsal views of a late meraspis skeleton; notice that the hypostoma is in place. x 8.5, U.C.M. 38741.



Explanation of Plate 17

Figures 1-31 - Phaseolops conus, n. sp.

1-3 - Anaprotaspides. 1, dorsal view of an incomplete shield, x 56, U.C.M. 38742a; 2,3, dorsal and ventral views of a complete shield; notice the posterior marginal doublure and a pair of posterior lateral spines, x 56, U.C.M. 38742b.

4-8,22 - Paraprotaspides. 4-7 are four shields all with undifferentiated pygidia; notice the facial suture and the palpebral lobes; 4,5, x 53, U.C.M. 38742c,d; 6, x 46, U.C.M. 38742e; 7, x 42, U.C.M. 38742f; 8,22, dorsal and ventral views of shield (associated with the shell of an ostracod), x 40, U.C.M. 38742g.

9-12 - Early meraspides. Four cranidia without pygidia, showing the distinct anterior borders and the posterior fixigenal borders; 9, x 46, U.C.M. 38742h; 10, x 34, U.C.M. 38742i; 11, x 34, U.C.M. 38742j; 12, x 30, U.C.M. 38742k.

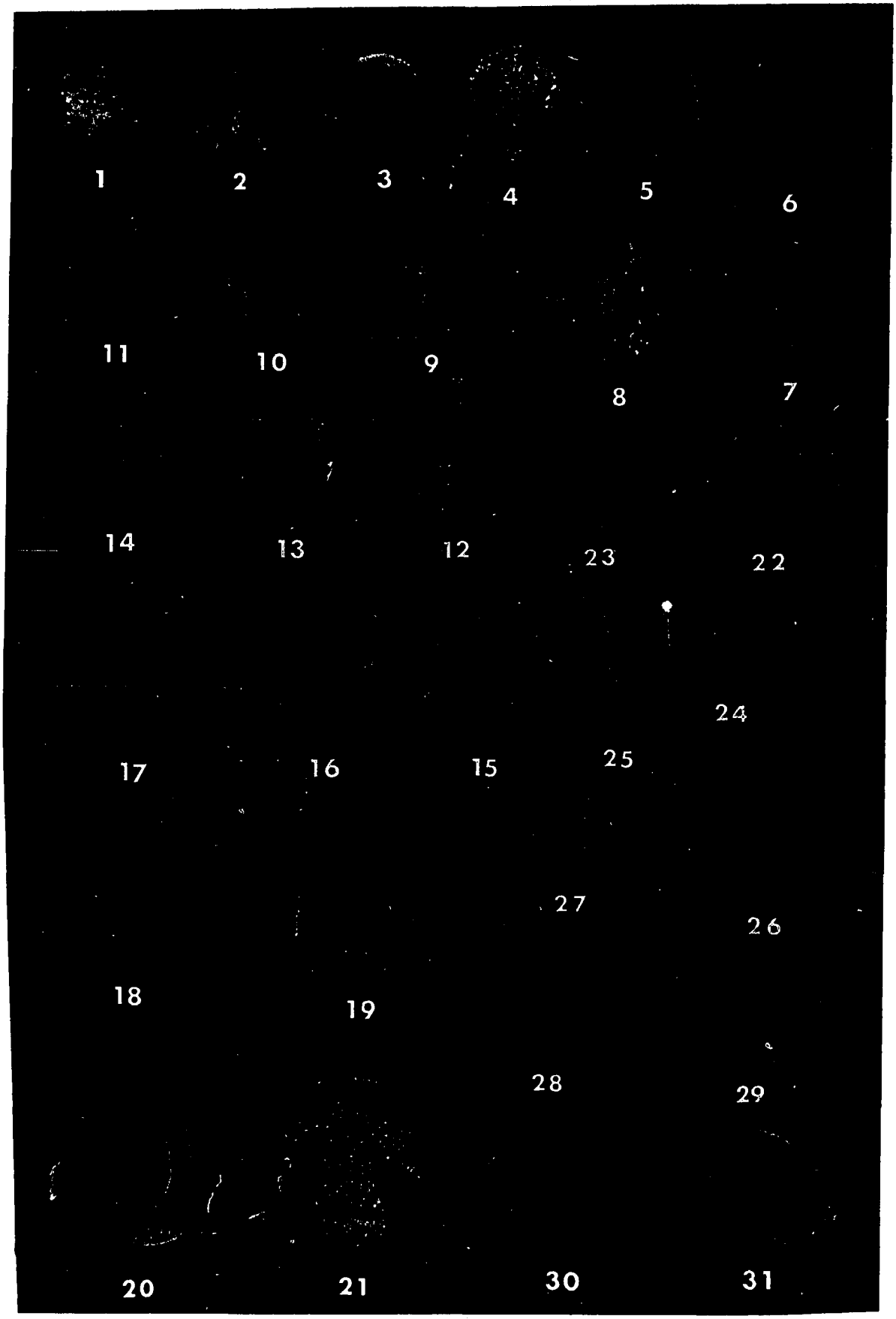
13-16,23,27 - Late meraspides. 13-16, a few incomplete cranidia, showing the well preserved preglabellar fields; 13, x 31, U.C.M. 387421; 14, x 27, U.C.M. 38742m; 15, x 28, U.C.M. 38742n; 16, x 20, U.C.M. 38742o; 23, a small librigena; notice the narrow ocular plate form, x 8, U.C.M. 38742s; 27, an incomplete pygidium, lacking marginal spines, x 26, U.C.M. 38742w.

17-21,24-26,28-31 - Holaspides. 17,18, top and side views of

a complete cranidium, x 13, U.C.M. 38742p; 19-21, three nearly complete cranidia; 19, x 13, U.C.M. 38742q; 20, x 12, U.C.M. 38742r; 21, x 21, U.C.M. 38742.

24-26 - Holaspid librigena; 24,26, two complete forms; note that the lateral furrows extend to the genal spines; 24, x 6, U.C.M. 38742t; 25, x 4, U.C.M. 38742u; 26, ventral view of a complete form, showing a broad doublure with distinct ridges along the border, x 4, U.C.M. 38742v.

28-31 - Holaspid pygidia. 28,29,31, three well preserved forms all showing three pairs of short marginal spines; 28, x 10, U.C.M. 38742x; 29, x 11, U.C.M. 38742y; 31, x 10, U.C.M. 38742z; 30, ventral view of a well preserved pygidium; notice the wide doublure and the ridges along the border, x 11, U.C.M. 38742a'.



Explanation of Plate 18

Figures 1-38 - Calliops strasburgensis Ulrich and Delo

1,2 - Paraprotaspis. Dorsal and ventral views of a complete instar, x 36, U.C.M. 38743a.

3-9 - Early meraspides. Notice the change in position of the palpebral lobes in small to larger specimens; 3, x 21, U.C.M. 38743b; 4, x 23, U.C.M. 38743c; 5, x 22, U.C.M. 38743d; 6, x 27, U.C.M. 38743e; 7, x 34, U.C.M. 38743f; 8, x 23, U.C.M. 38743g; 9, x 17, U.C.M. 38743h.

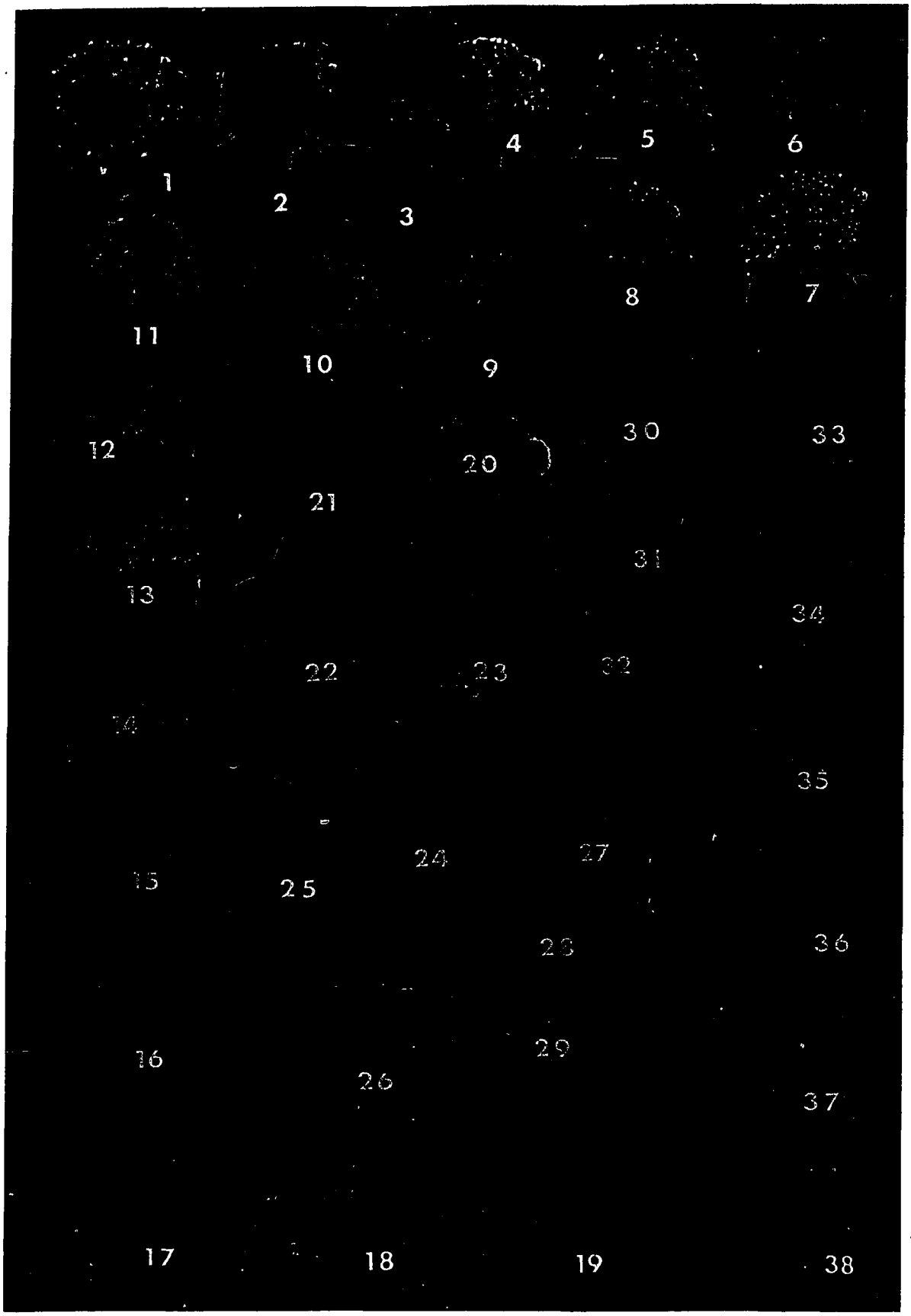
10-13 - Late meraspides. Notice the reduction of the spines and the increase in size of the palpebral lobes; 10, x 15, U.C.M. 38743i; 11, ventral view of a broken cranidium, x 14, U.C.M. 38743j; 12, x 8, U.C.M. 38743k; 13, x 10, U.C.M. 387431.

20,23,24,30,31 - Late meraspides. 20, a broken rostro-librigena showing the anterior marginal spines, x 25, U.C.M. 38743s; 23,24, ventral and dorsal views of two hypostomata, showing the narrow marginal doublure, posterior border, and a pair of posterior spines; 23, x 6, U.C.M. 38743u; 24, x 10, U.C.M. 38743v; 30,31, two pygidia bearing marginal spines; 30, x 20, U.C.M. 38743y; 31, x 6.1, U.C.M. 38734z.

21,22,25,28 - Holaspides. 21,22, anterior lateral and anterior views of a complete rostro-librignea, x 8.7, U.C.M. 38743t; 25, hypostoma, x 3.2, U.C.M. 38743r; 28, lateral oblique view of a thoracic segment, x 2, U.C.M. 38743x.

14,15,18,19,26,29,35,38 - Holaspides ("male"). 14,15, two crandia without rostro-librigenae; notice the small fixigenal spines; 14, x 3.5, U.C.M. 38743m; 15, x 32, U.C.M. 38743n; 18,19, two cephala with rostro-librigenae in place, notice the small fixigenal spines; 18, x 3.5, U.C.M. 38743; 19, x 3.2, U.C.M. 38743q; 26,29, side and frontal views of a less complete cephalon (the genal spines were broken off), x 2.8, U.C.M. 38743w; 35, ventral view of a less complete pygidium, x 4, U.C.M. 38743d'; 38, a complete pygidium, x 3.3, U.C.M. 38743g'.

16,17,27,32-34,36,37 - Holaspides ("female"). 16,27, dorsal and ventral views of a cephalon, x 3.1, U.C.M. 38743o; 17, a complete cephalon, showing no fixigenal spines, x 3, U.C.M. 38743p; 32, back view of a broken pygidium, x 3, U.C.M. 38743a'; 33, a medium sized pygidium, x 3.7, U.C.M. 38743b'; 34, a small pygidium associated with a few thoracic segments, x 11, U.C.M. 38743c'; 36,37, two well preserved pygidia; 36, x 3.8, U.C.M. 38743e'; 37, x 3, U.C.M. 38743f'.



Explanation of Plate 19

Figures 1-29 - Flexicalymene granulosa (Foerste)

1-4 - Anaprotaspides; showing two pairs of axial nodes and a longitudinal fissure; 1,2, x 53, U.C.M. 38744a, b; 3, an impression, x 52, U.C.M. 38744c; 4, x 52, U.C.M. 38744d.

5 - Paraprotaspis; showing the fusion of the axial nodes and the origin of the axial rings; notice the posterior portion of the shield without segmentation or differentiation, x 40, U.C.M. 38744e.

6-10 - Paraprotaspides. Notice the segmented protopygidium; 6, x 35, U.C.M. 38744f; 7, x 30, U.C.M. 38744g; 8, x 31, U.C.M. 38744h; 9, x 32, U.C.M. 38744i; 10, x 23, U.C.M. 38744j.

11,12,20 - Early meraspides. 11,12, two cranidia showing the himi-cylindrical glabella and absence of any pygidium; 11, x 25, U.C.M. 38744k; 12, x 26, U.C.M. 387441; 20, small pygidium possibly associated with 3 or 4 thoracic segments, x 30, U.C.M. 38744t.

13,14,16,21,25 - Late meraspides. 13, incomplete skeleton showing the conical glabella, x 14, U.C.M. 38744m; 14, incomplete cranidium showing the conical glabella, x 19, U.C.M. 38744n; 16, rubber mould of a cranidium, x 13, U.C.M. 38744p; 21, broken pygidium showing short marginal spines, x 24, U.C.M. 38744u; 25, hypostoma; notice a pair

of short broad posterior spines, x 20, U.C.M. 38744y.

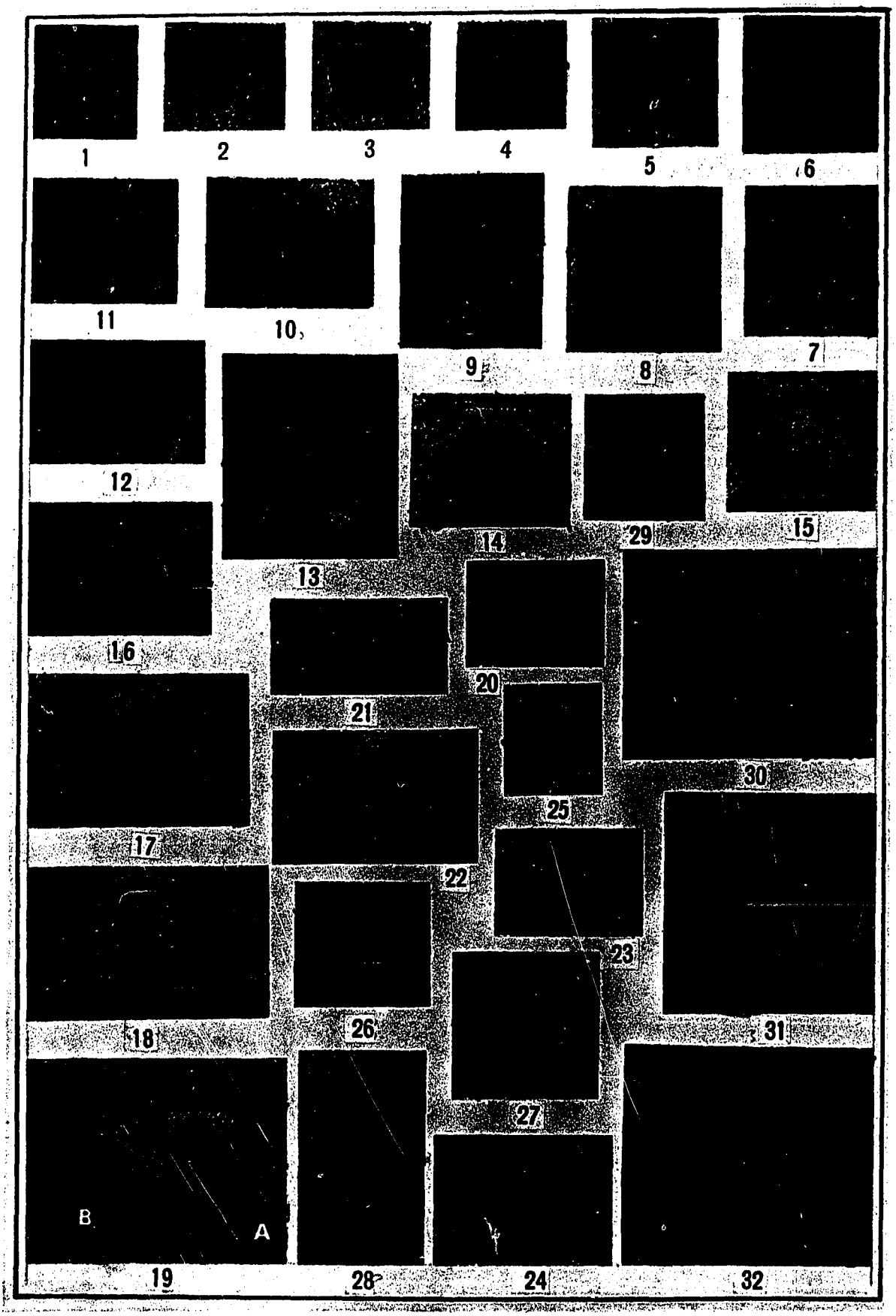
15,19A,24,29 - Holaspides ("female"). 15,19, two incomplete cranidia, showing the broader anterior borders; 15, x 15, U.C.M. 38744o; 19A, x 6.8, U.C.M. 38744s; 24, well preserved pygidium showing broader pleural lobes, x 8.4, U.C.M. 38744x; 29, a small librigena, x 13, U.C.M. 38744c'.

26,27 - Two hypostomata. 26, well preserved specimens; notice a pair of distinct pits on the anterior wings and the short posterior spines, x 5.9, U.C.M. 38744z; 27, x 14, U.C.M. 38744a'.

17,18,19B,22,23,28 - Holaspides ("male"). 17,18,19B, three cranidia; notice the narrower anterior border, x 8, U.C.M. 38744q; 18, x 4.2, U.C.M. 38744r; 19B, x 6.8, U.C.M. 38744s; 22,23, two complete pygidia with subtriangular outline, x 4.5, U.C.M. 38744v,w; 28, librigena, x 2, U.C.M. 38744b'.

Figures 30-32 - Flexicalymene meeki (Foerste)

Two individuals enrolled concentrically, the innter one is less incomplete, the outer one has the cephalon broken off. 30, side view; notice that the left one is complete, and the right one shows the thoracic segments and pygidium only. 31, dorsal view; notice that the inner one is on top, and the outer one, on the bottom; 30, ventral view, showing the weathered pygidia and cephalon. All x 2.1, U.C.M. 23263.



Explanation of Plate 20

Figures 1-13 - Cryptolithus bellulus (Ulrich)

1 - Paraprotaspis. Cranidium, showing a pair of palpebral ridges and eye tubercles; notice the anterior margin without fringe, x 23, U.C.M. 38745a.

2-5,10 - Early meraspides. Notice the shortening of the palpebral ridges and the expansion of the anterior fringe; 2, x 20, U.C.M. 38745b; 3, x 20, U.C.M. 38745c; 4, 19, U.C.M. 38745e; 5, x 8, U.C.M. 38745d; 10, small pygidium associated with two thoracic segments, x 18, U.C.M. 38745h.

6-8,11 - Late meraspides. 6, cranidium, showing the disappearance of the palpebral lobes and the tubercles, x 3.4, U.C.M. 38745f; 7, ventral view of a lower lamella; notice that the girdle extends into the genal spines, x 2.5, U.C.M. 38745g; 8, incomplete skeleton which shows four or five thoracic segments, x 5, U.C.M. 38745i; 11, pygidium which shows three distinct segments, x 12, U.C.M. 38745j.

9,12,13 - Holaspides. 9, a poorly-preserved cephalon; notice the fusion of the upper and lower lamella, x 1.8, U.C.M. 38745; 12,13, two pygidia showing the pleural lobe ridges, x 8.3, U.C.M. 38745j; x 3.7, U.C.M. 38745k.

Figures 14-31 - Isotelus stegops Green

17 - Anaprotaspis. Notice the longitudinal fissure along the central axis, x 57, U.C.M. 38746a.

18,19 - Metaprotaspides. Notice the well differentiated axial

lobes; 18, x 30, U.C.M. 38746b; 19, x 27, U.C.M. 38746c.

20,21 - Two paraprotaspides. Notice the elongation of the posterior portion; 20, x 20, U.C.M. 38746d; 21, x 26, U.C.M. 38746e.

14,15,22 - Late early meraspides. 14, a small pygidium, showing distinct axial and pleural furrows and terminal portion of the axis with elongate and concentric ridges, x 15, U.C.M. 38746o; 15, a less well preserved pygidium, x 8.3, U.C.M. 38746p; 22, cranidium with narrow preglabellar field and well-defined anterior border, x 13, U.C.M. 38746f.

23,24,27 - Late meraspides. 23,24, two cranidia showing no preglabellar field; 23, x 11, U.C.M. 38746g; 24, x 12, U.C.M. 38746h; 27, complete skeleton with seven thoracic segments only, x 3.4, U.C.M. 38746k.

16,25,26,28-31 - Holaspides. 16, a pygidium. Notice the disappearance of the distinct axial and pleural lobe furrows but presence of fine ridges, x 4, U.C.M. 38746q; 25,29, two "female" cranidia, x 2.1, U.C.M. 38746i; U.C.M. 38746e; 26, broken hypostoma, showing a pair of lateral pits and wrinkled surface, x 7, U.C.M. 38746j; 28, ventral view of an incomplete skeleton, x 1.7, U.C.M. 38746; 30, "male" cranidium; notice that it is wider and shorter than those of the "female" form, x 1.5, U.C.M. 38746m; 31, librigena showing the doublure and the well preserved median suture line, x 3, U.C.M. 38746n.