

THE PALEOZOIC EUMALACOSTRACA
of
NORTH AMERICA

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ABSTRACT

It has been assumed that the Paleozoic eumalacostracan Crustacea had morphological characteristics consistent with representatives of the extant "primitive" taxa, the Mysidacea and Syncarida. Morphological study of the American fossils proves this belief to be correct only for the Syncarida. The species with a carapace, though displaying morphological trends in the structure of the exoskeleton toward various established taxa, are distinguished not only by an unexpected combination of characteristics previously not known to exist in the same animal, but by some features known only in Recent Crustacea believed to be more primitive than Eumalacostraca. A complete revision of the classification with new genera and species: *Anthracaris*, n.g. (type species: *Anthrapalaemon gracilis* Meek and Worthen); *Mamayocaris jeffersi*, n.g., n.sp.; *Pseudoteallicaris*, n.g. (type species: *Teallicaris caudafimbriata* Copeland); *Anthracophausia strongi*, n.sp.; *Archaeocaris graffhami*, n.sp.; *Acadiocaris*, n.g.; (type species: *Palacocaris novascotica* Copeland) and *Palaeosyncaris dakotensis*, n.g., n.sp.; new families: Eocarididae, Palaeopalaemonidae, Anthracophausiidae, Pygocephalidae, Teallicarididae, Notocarididae, Anthracocarididae; new orders: Eocaridacea, Palaeostomatopoda, Anthracocaridacea, and a new superorder, Eocarida, is required.

Tagmosis of the body, modification of the exopod of the second antennae as a squama, jointing of the thoracic pereopods, development of a caudal fan through modification of the sixth pair of abdominal appendages as uropods, and reduction of the furca and median telson spine distinguish Eumalacostraca. These are characteristics of the nektonic "caridoid facies" superimposed upon a benthonic crustacean. The most ancient eumalacostracans reported in the literature are classified as syncarids. Re-interpretation and new discoveries prove these Devonian fossils are caridoid Malacostraca. True syncarids first occur in Upper Mississippian strata.

Recent Euphausiacea are specialized pelagic descendants of the most ancient Eumalacostraca. Decapods and the several orders of peracarids evolved from this stock in the late Paleozoic. Primitive morphological characteristics and the fossil record establish stomatopods and syncarids as a more ancient derivative which differentiated in the Devonian or early Mississippian.

INTRODUCTION

Despite the interest that has been shown in crustacean evolution, there has never been a critical morphological study of the Paleozoic Eumalacostraca.

Malacostraca are Crustacea with eight somites in the thoracic tagma and six or seven somites in the abdomen, the first antennae are biramous (rarely triramous), and the female gonopores are associated with the fifth thoracic somite and the male gonopores are associated with the eighth thoracic somite. Two primary subdivisions of this taxon are recognized; they are the Series Phyllocarida and the Series Eumalacostraca. Characteristics of the Eumalacostraca are: the exopod of the second antennae is developed

as a scale, the thoracic appendages are jointed (not foliaceous), there are six (not seven), abdominal somites, and the appendages of the sixth abdominal somite are developed as uropods. The most diagnostic character of the Eumalacostraca is the reduction of the furca and median spine on the telson which is replaced functionally by the caudal fan composed of the uropods and the body of the telson. The Recent Phyllocarida, the Leptostraca, have a carapace adductor muscle. This was probably absent in some of the extinct Archaeostraca, but proof is lacking that these Paleozoic fossils are truly malacostracans.

In the present study all fossil species from the United States are re-examined and described in detail. Specimens of only two of the Canadian species were received for direct examination; however, this work is comprehensive of all known American species. In the course of investigation, representative specimens of contemporaneous fossils from Europe, Africa, and Brazil have been studied, and information obtained has been synthesized into the discussion of interrelationships of the genera and the evolution of the Eumalacostraca.

Hundreds of excellent specimens in the ironstone concretions from the Pennsylvanian deposits of northern Illinois have been collected since the last American study (Packard, 1886) in which morphological interpretation of the Paleozoic Eumalacostraca was the primary objective. There are also many undescribed specimens from other deposits from Devonian to Permian in age that have accumulated in museum collections during the past 100 years. Dr. Percy E. Raymond, knowing of the great need for a biological study of these fossils, encouraged me to begin the work in 1948. As this study has progressed, morphology of the fossils has been compared with that of extant animals.

Knowledge of nearly the complete skeletal morphology of the basic types of Paleozoic Eumalacostraca represented by species in the Mazon Creek concretions has been realized in this work. Previous investigators failed to take advantage of the exquisite details preserved in the ironstone concretions because they neglected to prepare the fossils. The specimens are natural molds filled with soft flaky kaolin which must be removed before the fossils can be studied to advantage (compare photographs of unprepared and prepared

specimen, Plate 29, figs. 1, 2). Mineral materials filling the molds were removed under a binocular microscope with a needle sharpened to a chisel point and held in a pin vise. The cleaned specimens are difficult to study because they are concave impressions of the external morphology of the animals. Rubber latex, preferably red, has been used to duplicate the original form of the animal. No details are lost in the reproductions; the rubber duplicates minute setae and even the texture of the matrix. Not only is it easier to study the fossil as reproduced in positive relief, but superior photographs can be obtained if the red latex casts are covered by a thin film of ammonium chloride.

All available collections in the United States have been studied in pursuance of this investigation. The Peabody Museum at Yale University contains specimens that surpass, in numbers and preservation, the materials of the other museums. Specimens in principal museum collections are as follows: Peabody Museum, Yale University, 1711; U.S. National Museum, 99; Chicago Natural History Museum, 212; Museum of Comparative Zoology, Harvard University, 76; Illinois State Museum, 22, and Princeton University, 184. Types and specimens of rare species in other collections are referred to in the text.

It has been assumed that the Paleozoic Eumalacostraca had morphological characteristics consistent with representatives of the extant "primitive" taxa, the Mysidacea and the Syncarida (Woodward, 1907 b; Peach, 1908; and Calman, 1896, 1911 b, 1932 a and b). Re-study of the fossils from Mazon Creek proves this belief to be correct only for the Syncarida. Once the morphology of the basic types of Paleozoic Eumalacostraca is established, it is possible to re-interpret the species represented less adequately by compressions from other deposits. This study results in the recognition of four new genera. From the morphological characteristics discovered, it is evident that a complete revision of the classification is required. New families, orders and a new superorder must be proposed for the systematic classification of the known Paleozoic Eumalacostraca.

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Rare Recent specimens of the Tasmanian mountain shrimp, *Anaspides tasmaniae* Thomson, have been received for morphological study from Mr. Edgar F. Riek, Canberra, Australia. A specimen of the deep sea shrimp, *Gnathophausia gracilis* Suhm, was obtained for dissection from Dr. W. D. Clarke of the Scripps Institution of Oceanography. Dr. Elizabeth Deichmann of the Museum of Comparative Zoology has made available many specimens for my reference.

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EXPLANATION OF MORPHOLOGICAL TERMINOLOGY

Terminology in carcinological works varies slightly from taxon to taxon. Because the Paleozoic Eumalacostraca display morphological trends of differentiation toward all the modern types, the terms herein used are not completely in accord with those of any one author; a single term must be employed consistently for the same homologue. Terms have been chosen based upon usage, descriptive appropriateness, and brevity. They have been selected from those used by Sars (1885, p. 3-6), Calman (1909), Hansen (1925, p. 83-89), Tattersall and Tattersall (1951, p. 13-28), and Snodgrass (1956).

Theoretical implication in morphological terminology cannot be completely avoided. For example, the carapace mantle originates ontogenetically as a fold of the integument at the posterior margin of the cephalon. Some authors (*i.e.*, Borradaile and Potts, 1958, p. 350) would differentiate the head shield from the carapace by the position of the cervical groove and term the complete cephalothoracic structure the dorsal shield. This introduces an error. The dorsal musculature of the two posterior cephalic appendages, the first and second maxillae, originates posterior to the cervical groove; thus this cannot be used as a criterion for division. The prominent sulcus that traverses the cephalic shield is a homologous structure throughout the Eumalacostraca. In the Syncarida it can be seen to be associated with the mandibles. The term mandibular sulcus should be abandoned unless it is to be employed only for the anterior sulcus on those Crustacea, *e.g.*, *Acanthotelson* and *Palaeopalaemon*, in which the cephalic sulcus bifurcates into an anterior branch and the cervical groove. Consistent with classical usage, the complete dorsal shield of the cephalothorax is termed a carapace in this work. In those forms without the thoracic mantle, the cephalic shield is an appropriate name for the dorsal skeletal covering of the head.

Tagmosis in the Eumalacostraca does not depart from a basic plan. Five pairs of appendages are borne on the head; they are first antennae, second antennae, mandibles, first maxillae, and second maxillae. The stalked compound eyes are not homologous with appendages. In this work a practical scheme has been followed and

the somites are correlated with the appendages they bear. Thus the cephalic tagma is considered to consist of five somites, the thorax eight somites and the abdomen six somites and a telson. The adult eumalacostracan body is composed of a total of 19 appendage-bearing somites and a telson which may bear a furca and a median articulated spine. These somites have been indicated by Roman numerals on the morphological drawings. It is true that cephalization has occurred in some Recent eumalacostracans such that one or two thoracic somites have been incorporated into the cephalic tagma, e.g., *Anaspides* and *Gammarus*, or fusion has occurred between the telson and the last abdominal somite, e.g., *Bathynella* and *Tanais*. The appendages of the fused somites are an infallible criterion for their identification.

Structures that appear in embryonic and larval stages of some Recent eumalacostracans should be given special consideration in the study of the Paleozoic fossils. They are: a seventh abdominal somite and a furca and median spine on the telson. The seventh abdominal somite and the furca are significant because it is believed the ancestral malacostracan had these characteristics, as does the Recent Leptostracan, *Nebalia*. Manton (1928, p. 446) reported the presence of a seventh abdominal somite as "represented in the embryo (*Hemimysis lamornae*) by a pair of mesoblastic somites and a ganglion, although in the adult it is completely fused with the sixth segment." She (1928, p. 446-447) dismissed the furca on the embryo of *Hemimysis* as "purely ectodermal and does not appear to be a pair of appendages . . ." Evidence of a seventh abdominal somite is not present on any of the Paleozoic primitive Eumalacostraca so it is doubtful that Manton's observations are of phylogenetic significance. On the other hand, all fossils except the syncarids have a pair of furcal lobes and a median spine on the telson. A furca is known in adult Recent Eumalacostraca only on euphausiids and the syncarids of the Order Bathynellacea. The median spine is known only in the adults of euphausiids. Gurney (1942, p. 116-123) noted the occurrence of these structures of the telson in ontogenetic stages of the Eumalacostraca and concluded they are relics of a "primitive form of telson preserved from a predecapod ancestor." The paleontological evidence presented herein proves his deduction.

It has been assumed that the primitive crustacean leg had a

sympod with three joints because the sympod of the first antennae of all Crustacea typically consists of three joints, and three joints are allegedly present on the thoracic legs of species of taxa other than the Copepoda. It is only in the copepods that bifurcation into two rami, an endopod and an exopod, characteristically occurs at the third joint. Some authors have interpreted a precoxal joint on many Crustacea where one does not exist. Embryological evidence (Heegard, 1946, p. 2-4) and the discovery of only a single joint in the sympod of the primitive appendages of *Hutchinsoniella* (Saunders, 1957, p. 120-124), *Spelaeogriphus* (Gordon, 1957, figs. 21-26), and *Thermosbaena* (Siewing, 1957, p. 258) have emphasized the need for a re-evaluation of concepts of interpretation of the crustacean limb. In the Paleozoic fossils only one joint could be distinguished in the sympod of the species with a carapace.

The articulation of greatest flexure of the thoracic endopod is consistent in position. This "knee" is the articulation between the fourth and fifth joints of the leg, the merus and carpus, in those forms that have two joints in the sympod. There are a few exceptions in Recent Crustacea where fusion or additional joints have been introduced to complicate the primitive plan. However, Hansen (1925, p. 89) was correct in believing the "knee" is of the greatest importance in determining the homology of the joints of the endopod.

For purposes of homologous comparison between the different Eumalacostraca, the syncarid appendages are most useful (Text Plate 1). The thoracic appendages are biramous with the exopod arising from the second discreet joint. The elusive theoretical precoxal joint has not been seen. From the basal joint, the coxa, two lobate, membranous epipods originate. The exopod arises from the second joint, the basis, and consists of a stipe and a flagellum. The endopod is divided into five joints; they are: ischium, merus, carpus, propodus and dactylus. The "knee" is between the merus and carpus. Three joints are distal to it.

Appendages of the Paleozoic syncarids have an identical structure. The Paleozoic eumalacostracans with a carapace are believed to have had thoracic appendages of comparable structure but with only one joint in the sympod. So that the numbering system employed herein for the joints of the thoracic appendages would indicate homologous parts, the single sympod joint of these Crustacea

has been indicated as the second leg joint though it represents both the coxa and the basis.

For morphological comparative purposes, drawings of the skeletal structure of the Recent syncarid, *Anaspides tasmaniae* Thomson are presented (Text Pl. 1 and Text Pl. 14, fig. b). Except for the absence of a carapace, marsupium, and furcal lobes and a median spine on the telson, this species portrays the morphological features of the fossil Crustacea to be described. The skeletal features of the cephalothorax of a primitive Recent lophogastrid mysidacean, *Gnathophausia gracilis* Suhm, with a carapace are shown in Text Pl. 14, fig. c. The abbreviations and symbols employed on these figures and throughout this work are:

| | |
|--------|-----------------------------------|
| A, | opening of otocyst |
| Abd, | abdomen |
| An, | anus |
| Ant, | antenna, (1 Ant and 2 Ant) |
| As, | antero-lateral spine |
| B, | branchial area of carapace |
| brC, | branchial chamber |
| Bs, | branchiostegal spine |
| C, | cardiac region of carapace |
| Cp, | carapace |
| Cps, | cephalic shield |
| Cs, | cardiac spine |
| cvg, | cervical groove |
| Dblr, | doublure |
| E, | eye |
| Endpd, | endopod |
| Endt, | endite |
| Eppd, | epipod |
| Epst, | epistome |
| Expd, | exopod |
| F, | foramen (with appropriate prefix) |
| Fl, | flagellum |
| G, | gastric region of carapace |
| gnL, | gnathic lobe of mandible |
| Gpr, | gonopore |
| Gs, | gastric spine |
| H, | hepatic region of carapace |
| Hs, | hepatic spine |
| K, | "knee" between merus and carpus |
| Lm, | labrum |
| Md, | mandible |
| mol, | molar process of mandible |
| Mx, | maxilla (1 Mx and 2 Mx) |
| Mxpd, | maxillipod |
| Npr, | nephropore |
| O, | ocellus |
| Os, | supraorbital spine |

| | |
|---------|----------------------------------|
| Ostg, | oostegite |
| Pa, | ocular papilla |
| Pgn, | paragnath |
| Pl, | pleural lobe of tergite |
| Plp, | palp |
| Plpd, | pleopod |
| Prpd, | pereiopod |
| R, | rostrum |
| S, | antennal scale or exopod, squama |
| Sp, | sternal process |
| Sr, | seminal receptacle |
| St, | sternum |
| Sy, | sympod, protopod |
| T, | tergite |
| Tel, | telson |
| telS, | telson spine |
| tell, | telson lobe, furcal lobes |
| Urpd, | uropod |
| 1...8 | thoracic appendages |
| 1...7 | joints of thoracic appendages |
| 1...XIX | body somites |

In the descriptions, observation of morphological detail is substantiated by reference to specific fossils on which the feature is best displayed. Citations of the institution in which the specimens are preserved have been abbreviated. They are:

| | |
|-------|---|
| CMNH | Chicago Museum of Natural History |
| CIMNH | Cleveland Museum of Natural History |
| CU | Columbia University, New York |
| GSC | Geological Survey of Canada, Ottawa |
| ISMNH | Illinois State Museum of Natural History, Springfield |
| MCZ | Museum of Comparative Zoology, Harvard University |
| PU | Princeton University |
| PY | Peabody Museum, Yale University |
| USNM | United States National Museum |
| UI | University of Illinois, Urbana |
| UO | University of Oklahoma, Norman |

DESCRIPTIONS OF THE PALEOZOIC EUMALACOSTRACA

SPECIES WITH A CARAPACE

Until recently the most ancient authentic eumalacostracans reported in the literature were classified as syncarids and, therefore, supposedly lacked a carapace. They are *Palaeocaris destinezi* Van Straelen, 1943, from the Upper Devonian of Belgium and *Palaeocaris cuylerensis* Wells, 1957, from the Middle Devonian of New York. Morphological evidence is indicative of the caridoid facies for

these species and the new genus, *Devonocaris*, was proposed for them (Brooks, 1962 a). In the same paper a specimen with the carapace preserved was described from the Middle Devonian of Germany. This new crustacean, *Eocaris oervigi* (Text Pl. 9, fig. e), has its closest affinities with *Palaeopalaemon newberryi* Whitfield (1880) from the Upper Devonian of Ohio.

Though the carapace provides the best diagnostic characteristics for definition of genera, its absence from poorly preserved fossils is negative evidence. Because of this, several fossils are in need of reinterpretation. Not only were the "Devonian syncarids" incorrectly interpreted, but *Belotelson magister* Packard (1886 a) from the Pennsylvanian of Illinois, has characteristics of the caridoid Crustacea. On the other hand, *Squillites spinosus* Scott (1938) from the Upper Mississippian of Montana is obviously a syncarid. It and an associated new genus are the most ancient eumalacostracans known without a carapace. *Anthracocharis scotica* (Peach) from the Mississippian of Scotland (Calman, 1932 b) and a contemporaneous species from Canada have a reduced carapace comparable to that of the Spelaeogriphacea and Tanaidacea.

Because the Paleozoic Eumalacostraca have not been adequately studied, diversion from objective description is sometimes necessary to evaluate the validity, significance, and theoretical implication of new observations. Without doing this, it would be impossible to interpret the fossils accurately.

The species with a carapace, though displaying morphological trends in the structure of the exoskeleton toward the various modern eumalacostracan taxa, are distinguished not only by an unexpected combination of characteristics previously not known to exist in the same animal, but by some features previously known only in Recent Crustacea believed to be more primitive than the Eumalacostraca. Therefore in the descriptive portion of this study no attempt has been made to arrange the genera systematically. The basic division is between those that are known or believed to have had a carapace and those that do not. Because of the inadequacy of many of the fossils, the species with better preservation, in which the morphology can be more completely determined, are described first. Genera that are closely related are grouped together. Otherwise the arrangement is, more or less, from youngest to oldest.

A complete systematic revision of the Paleozoic Eumalacostraca is presented after all the basic morphological types are redescribed.

Genus **ANTHRACARIS**, new genus

The singular nature of the species described as *Anthrapalaemon gracilis* by Meek and Worthen is herein proven. The species has affinities with the fossils assigned to *Pygocephalus* Huxley (1857) and its synonym *Anthrapalaemon* Salter (1861); however, it is distinguished (Text Pl. 2) by the presence of a pair of spines on the hepatic region of the carapace, the sympod of the first thoracic appendage is not unlike those succeeding. There are large endites on the sympods of both the first and second thoracic appendages, the endopod of the third thoracic appendage is not fully developed as a pereopod, and there is an absence of oostegites. A large seminal receptacle is present on the last thoracic sternite of the females of both genera. The generic name *Anthracaris* is proposed to distinguish this crustacean; the incongruity of which was noted by Packard (1885 b) in proposing the family Anthracaridae. From the many excellent specimens now available in the concretions from Mazon Creek, Illinois, the type species, *Anthrapalaemon gracilis* Meek and Worthen, will be described in detail.

A comma is inserted in the synonymy in place of repetition of the original author's name.

Anthracaris gracilis (Meek and Worthen), 1865 Pls. 29-43; Pl. 44, fig. 4; Text Pl. 2; Text Pl. 3, figs. a-c

Anthrapalaemon gracilis Meek and Worthen, 1865, p. 50-51.

Anthrapalaemon gracilis, Meek and Worthen, 1866, p. 406-408, pl. 32, fig. 4.

Anthrapalaemon gracilis, Meek and Worthen, 1868 b, p. 554, figs. a, b.

Anthrapalaemon gracilis, White, 1884, p. 180, pl. 38, figs. 8, 9.

Anthrapalaemon gracilis, Packard, 1885 b, p. 880-881.

Anthrapalaemon gracilis, Packard, 1886 c, p. 135-140, pl. 7, figs. 3, 3 a, 4, 4 a, 5, 6.

Anthrapalaemon gracilis, Van Straelen, 1931, p. 24.

Because the genus is monotypic, the description of the specimens must replace the specific diagnosis.

Description of the specimens.—One hundred eighty-three ironstone concretions containing specimens of this species have been

studied, of which three are from the collection of Worthen.¹

Two specimens, not counterparts, have been labeled types; one is at the University of Illinois, X-343 (ISMNH 11124) and the other is in the Illinois Geological Survey collections (ISMNH 3067). At the time Meek and Worthen's original study was made only one specimen was available. This was poorly illustrated by an engraving (1866, pl. 32, fig. 4). The description of the species was revised by Meek and Worthen (1868 b) after several specimens had been received. Restorations based on the composite information from all of the specimens were presented in wood cuts (1868 b, p. 554, figs. a, b), but they refer to no single specimen. Only one specimen in the Worthen collection can be considered a primary type and this is the holotype. The specimen which has been mislabeled as a type in the collections of the University of Illinois, X-343 (ISMNH 11124, Pl. 30, fig. 4) bears no resemblance to the specimen drawn by Meek and Worthen. It is probable that the specimen from the Illinois Geological Survey (ISMNH 3067, Pl. 30, fig. 1) is the holotype. The general shape, the size, and the poor preservation of the caudal extremity conform to the description, measurements, and illustration originally presented; however, many details well portrayed by this specimen were not mentioned or illustrated in the 1865 and 1866 papers.

All four of the specimens figured by photographs in Packard's (1886 c, pl. 7, figs. 3, 3 a, 4, 4 a, 5, 6) work are in the collections of the U.S. National Museum. They are catalogued as USNM 38843. Better photographs of two of these plesiotypes are presented (Pl. 30, figs. 3, 5).

Preservation of most of the specimens is suggestive of a relatively stiff unmineralized chitinous exoskeleton. In all cases, the skeletal materials have deteriorated. If the exoskeleton was mineralized during life, it is doubtful the skeletal remains could be distorted, as many of the specimens have been, without rupture. Sternal features are impressed onto the dorsal surface of the carapaces of

¹Note: Upon retiring as State Geologist of Illinois, Worthen withdrew his collection from the Illinois State Museum. They were listed and offered for sale by his heirs, see Worthen and Worthen, 1889. Most of the specimens are now in the collections of the University of Illinois.

many of the specimens, *e.g.*, Pl. 31, fig. 1. This is a characteristic of fossil insects, arachnids and other arthropods with chitinous exoskeletons lacking mineral reinforcement. Considerable wrinkling of two specimens is illustrated (Pl. 32, fig. 2; Pl. 41, fig. 1).

During deterioration of the chitinous materials of some of the specimens, a complex pattern of fractures (Pl. 32, fig. 1) was produced resulting in a reticulate pattern. That this mosaic of both the carapace and the tergites of the abdomen is not a feature of the original exoskeleton is proven by its absence on many of the specimens, by the negative relief of the reticulate pattern, and by inconsistency and asymmetry of design.

Another feature of preservation that may be confused with original structure of the exoskeleton is small mammilla-like protrusions on the dorsal surface of the carapace. They are conspicuous near the lateral margins of only a few specimens. Lack of a pattern of distribution and the unsymmetrical occurrence on the left and right sides of the specimens prove their fortuitous nature. From examination of the nodules it was determined that the "mammillae" correlate with sites of soft ochreous material. Their origin is related to small crystals of pyrite that have weathered.

Statistical analysis of this species has been complicated by distortion of the fossils. Most specimens are preserved in a dorsal-ventral position and have undergone considerable compression. Only five percent of the specimens are preserved on their sides in the position that Glaessner (1929) argued represent positions assumed by exuviae, *e.g.*, PY 19998 (Pl. 35, fig. 4). That they are remains of cadavers and not exuviae is suggested by detrital fillings of the alimentary canal. If some of the fossils were exuviae, the sample would not be representative of the original population. Significant dimensions have been determined with a vernier caliper and recorded for all specimens on which plausible measurements could be made. For some features this represented a small percentage of the total sample.

The parameters measured are the ones that can be reliably determined most frequently on the fossils. The body length is the total length from the anterior margin of the carapace at the base of the rostrum to the suture at the base of the median telson spine.

The length of the carapace was measured in the sagittal plane and does not include the rostrum. The position of the cervical groove is reported as the distance forward from the posterior edge of the carapace in the sagittal plane. Rostrum length, in the few cases that its complete length could be determined, was measured from the tip to the anterior edge of the carapace. The maximum width was measured as the greatest breadth at a position about one-half way back on the carapace. The anterior width was taken as the distance across the carapace at the base of the antero-lateral spines and the posterior width as the interval across at the postero-lateral angles. The length of the antero-lateral spines was measured from the anterior edge of the carapace to the pointed tip. Serrations on the branchiostegal keel were recorded for only those specimens on which the total number could be seen.

Measurements and proportions of representative specimens, including the alleged "types" are given in Text Plate 3, fig. d. Statistical analysis based on the total number of observations of each parameter (N), maximum size (Max), minimum size (Min), mode (Mo), median (Me), arithmetic mean (Ma), and standard deviation (S) is included in the table for characteristics of value in defining the species.

Anthracaris gracilis was a small crustacean. The maximum body length measured was 37 mm. (PY 19937) and the minimum was 16 mm. (PY 19983, Pl. 35, fig. 2). When the body length in percentage frequency is plotted graphically in millimeters, and a line graph drawn, size groupings of units of 3 mm. are evident (Text Pl. 4, fig. a). What appears to be an arithmetic progression is actually a geometric progression with a value of about 1.1. This progression may represent stages of growth. For larval and immature Crustacea, the increase in size of each moult is by a factor of about 1.25 (Brooks' rule, Teissier, 1960, p. 541), but the rate of growth decreases as maturity is reached. The low value suggests we are dealing with mature individuals.

The data plotted as a histogram (Text Pl. 4, fig. a), using class intervals of 3 mm. of body length, show a distribution skewed toward the larger sizes. This is normal for adult populations of invertebrate animals and reflects their growth and mortality. The

clustering of the observations about a single mode with a value of 31 mm. indicates only one species was represented in the population. It also proves that there was no sexual dimorphism in size.

The carapace is the part of the animal most frequently found and upon which most of the fossil genera have been characterized. No single specimen reveals all of the features of the carapace. The restorations (Text Pl. 2, 3, fig. a) are composites based especially upon the specimens figured on Plates 31 to 35. Most of the specimens have been spread laterally. The least compressed is PY 19941 (Pl. 33, fig. 2) in which the body depth is about one-half the width of the carapace. Though this is somewhat less than the original relationship, the animals were definitely applanated.

Because of deformation, the most reliable measurement of the carapace is its length. Its mode value is 14.5 mm. but the variation is skewed (Text Pl. 4, fig. c). Due to deformation and inaccuracies in size determination, no growth stages could be detected. The mode of the proportion of the carapace length to the body length is 0.5; however, the median and arithmetic mean value of 0.46 is a more reliable index of the original relationship. The maximum width of the carapace is about nine-tenths its length. The maximum and anterior widths of the carapace and the rostrum length are plotted against the length of the carapace in Text Plate 4, fig. b. The line ($Y = 0.6 X$) about which the values of the anterior width to length are distributed has a lower slope and is divergent from that of the line of the anterior width of the carapace ($Y = 0.9 X$). Though the geometric growth rates for both width measurements are constant with relation to the carapace length, the relationship between the two dimensions is allometric. In practically all specimens the posterior width of the carapace is the same as the anterior width.

It has been assumed in studies of related genera that the apparent margins were the true lateral edges of the carapace. What appears to be the margins are branchiostegal pleural keels. Ventral to the keel the carapace is abruptly underfolded. The ventral edges lie against the flanks of the thoracic somites just above the coxa of the legs to form a crablike branchial chamber. A doublure is unmistakably present on PY 19989 and MCZ 5229 (Pl. 35, fig. 1; Pl. 41, fig. 1).

The pleural keels are serrate anteriorly. The small denticles diminish in size posteriorly and the posterior two-thirds of the keel is smooth. Only 26 specimens are preserved so that all serrations can be counted. About one-third of the specimens have eight denticles but the range is from five to eleven. One would expect the number to be fixed or to increase with growth, but no relationship with size exists (Text Pl. 4, fig. d). Though most specimens have equal numbers of serrations on the left and right keels, some individuals have them unequally developed; for example, PY 19932 (Pl. 31, fig. 1) has eight denticles on the left side and ten on the right.

The lateral keels are produced into acute spines at the antero-lateral angles of the carapace. When well preserved their tips are pointed as on PY 19932 (Pl. 31, fig. 1). Exact measurements are difficult to obtain, but in the best specimens their length is about one-eleventh to one-twelfth the length of the carapace.

The anterior margin of the carapace is best displayed by PY 19993 and PY 20003 (Pl. 34, fig. 1; Pl. 32, fig. 1). Immediately inward from the antero-lateral spines, the margin is recessed and then projects slightly forward to a central portion of about one-half the width of the carapace. This portion of the anterior border is straight and at right angles to the axis of the plane of symmetry. From this, the rostrum arises abruptly through an arc of small radius.

At the center of the anterior margin of the carapace a long spinelike rostrum projects anteriorly. It is well preserved in PY 19993, PY 20003 (Pl. 34, fig. 1; Pl. 32, fig. 1) and in PY 19928 (Pl. 35, fig. 3) which presents a side view. The rostrum arises in the mid-dorsal line about a quarter of the distance back on the carapace through anterior development of a mid-dorsal keel. The rostrum in cross section is in the form of an inverted T consisting of a central keel and lateral flanges. The central keel has its greatest development just anterior to where the margin of the carapace gives way to the lateral flanges. The transverse flanges are widest at the base. The keel and flanges taper to a point anteriorly with the extremity slightly upturned. No trace of serrations on the dorsal keel or the flanges was observed. From the margin of the carapace to the tip of the rostrum is slightly over one-half the length of the carapace. In PY 19992 it is 0.58 and in PY 19993 it is 0.59 of the carapace length. For

the eight specimens in which this proportion could be determined, the mode, median, and arithmetic mean were 0.60.

The features of the dorsal surface of the carapace are: a posterior mid-dorsal keel, transverse cervical groove, marginal pleural flanges, a pair of gastric spines and a pair of hepatic spines. The mid-dorsal keel is a raised reinforced line. It arises midway back on the carapace posterior to the hepatic eminences. The cervical groove divides the carapace transversely. The groove is situated forward on the carapace at a distance of three-quarters of its length. From the mid-dorsum, the groove extends anteriorly and laterally. Though it appears to bifurcate into anterior and posterior prongs on some specimens, it terminates at the site of apparent splitting. The supposed anterior and posterior prongs are the division between the pleural flanges and the arched main body of the carapace. That the anterior and posterior furrows do not exist is well shown by PY 20003, PY 19996, and PY 19975 (Pl. 32, fig. 1; Pl. 36, fig. 1; Pl. 32, fig. 2). Compression has caused furrows to develop in some specimens at the juncture between the central and lateral regions of the dorsal surface of the carapace.

A pair of prominent spines is situated on the protocephalic portion of the carapace, vide PY 20003 and PY 19988 (Pl. 32, fig. 1; Pl. 33, fig. 1.). In the morphological terminology of Recent Malacostraca, these are referred to as gastric spines. Posterior to the cervical groove a pair of spines arise through development of ridges. It is common to refer to similarly situated structures as hepatic spines. The position and ridgelike nature of the bases of the hepatic spines are shown by PY 19975 and PY 19941 (Pl. 32, fig. 2; Pl. 33, fig. 2).

The posterior margin of the carapace is usually not well preserved. It can be seen on PY 19941 and PY 19975 (Pl. 33, fig. 2; Pl. 32, fig. 2). The border seemingly fitted closely around the tergite of the first abdominal somite, though in most specimens the posterior lateral angles have been spread by compression resulting in a posterior flare of the carapace. The posterior margin was originally highly arched. When viewed from above it is slightly arcuate being concave forward. This concavity is accentuated in compressed specimens. As is the case with all crustacean carapaces, its edges are reinforced.

That the carapace was not fused with the posterior thoracic somites is shown by several specimens lying on their side in such orientation that their free unattached nature is manifest by the carapace being displaced upward away from the thorax, vide PY 19928 (Pl. 35, fig. 3). The granular undersurface of the carapace can be seen on PY 19928 (Pl. 40, fig. 2). It also shows that the thoracic somites retained their identity. Lack of fusion is further proven by the freely jointed sternites which are commonly separated in the fossils as on PY 19947 (Pl. 40, fig. 3).

Features that may be mistaken for characteristics of the carapace are especially well shown by the dorsal surface of PY 19932 (Pl. 31, fig. 1). In this specimen the sternites of the thorax have been impressed against the undersurface of the carapace. The outlines of the sternites are expressed as transverse ridges. The raised central portion of the carapace upon which the ventral features are reflected is bounded laterally by distinct lines. The lines bordering the raised area are an outline of the thorax, especially the sternum, and have been produced through compression. These features have been mistaken (Salter, 1861, and Rhodes and Wilson, 1957) as characteristics of the carapace of the species of *Pygocephalus* (= *Anthrapalaemon*) (Text Pl. 6, figs. b, c). Compare the raised area on the carapace of *A. gracilis* with the thoracic sternites of the same specimen (Pl. 31, figs. 1, 2). For the normal aspect of the carapace in which the sternal features have not been superimposed see the carapaces of PY 20003 and PY 19975 (Pl. 32, figs. 1, 2).

The surface of the carapace of typical individuals is believed to have been without ornamentation. Under magnification the smooth impressions of the surface texture are finely granulate. This is especially well shown by specimens CMNH 28125 and MCZ 5206 in which impressions of the original carapace surface are superbly preserved. The mammillae on the marginal flanges of PY 19932 are due to crystals of weathered pyrite; however, the tubercles distributed over most of the dorsal surface of the carapace of PY 19975 (Pl. 32, fig. 2) may be authentic ornamentation. If so, this is a variant as this specimen differs in no other way from typical specimens of *A. gracilis*.

The skeletal features of the head are remarkably well preserved on some of the specimens of *A. gracilis*. The sensor region of the

head, the protocephalon, bears a pair of stalked compound eyes and two pairs of antennae. Three additional somites are fused into the cephalic tagma. These gnathic somites bear the mandibles and two pairs of maxillae.

The ventral skeleton of the protocephalon can be seen on many specimens but is decipherable on only a few. A composite drawing of the ventral aspect of the head with all the appendages removed, except the mandibles, is presented in Text Pl. 3, fig. b. The ventral plate of the protocephalon, or epistome, with foramina for a pair of stalked eyes and two pairs of antennae are shown as seen on USNM 38842-200¹¹ (Pl. 44, fig. 4). First antennae are seen to originate from the protocephalon on PY 19931 (Pl. 40, fig. 1). In this specimen the portion from which the first antennae arise is separated from the portion bearing the second antennae. The separation has occurred along a suture which can be seen on USNM 38842-200¹¹, PY 20022 (Pl. 42, fig. 1) and USNM 38843 (Pl. 39, fig. 1).

Just anterior to the labrum is a transverse prominence joined to the second antennal "sternite" of the epistome by a suture. In Pl. 40, fig. 1, the relationship of this to the mandible articulation is shown. The strong development of the epistome corresponds to a similar development in Recent decapods, *e.g.*, *Cambarus longulus* Girard, in which a supralabral ridge exists to support the secondary articulation of the mandible.

It is easy to mistake portions of the peduncle of the first antennae for eyes as did Meek and Worthen in their original study. Both stalked eyes are present on PY 19694 but are too poorly preserved to photograph. A stalked eye is present on the left side of PY 19993 (Pl. 34, fig. 1). Doubts of the validity of interpretation of these indefinite remains are dispelled by the presence of the foramina on USNM 38842-200.¹¹ Also, stalked eyes are well preserved on a closely related genus to be described below, see Pl. 44, figs. 2, 3.

The thick basal peduncle, sympod, of the first antennae consisting of three segments is commonly preserved, *vide* PY 20022 (Pl. 42, fig. 1). The flagella are more rarely present. All or part of both the outer and inner flagella are preserved in PY 19931, 19936,

19939, 19944, 19945, 19988, 19990, 19998, 20001, 20003, 20013 and MCZ 5224. PY 19988 (Pl. 33, fig. 1) has the sympod and portions of both flagella preserved. The basal joint of the peduncle is long, and the two distad joints are short and about equal in length. A row of setae originates on the inner margins of these joints. Their presence in life is indicated by a row of about ten setal sockets on the inner edge of both short joints of PY 19996 and PY 20000. Some of these sockets can be seen in the photograph of PY 20022 (Pl. 42, fig. 1). The inner flagellum is short, being about one-sixth the length of the animal. It consists of 18 annuli of equal length but of diminishing diameter. The length of the outer flagellum is about one-third the length of the animal. In specimen PY 19932 (Pl. 31, figs. 1, 2), 64 annuli of equal length constitute the tapering flagellum.

The second antennae are present on many of the specimens; especially good are USNM 38843, MCZ 5229, PY 19929, PY 19931, PY 19932, PY 19988, PY 19993, and PY 20022 which are figured (Pl. 39, fig. 1; Pl. 41, fig. 1; Pl. 43, fig. 1; Pl. 40, fig. 1; Pl. 31, fig. 1; Pl. 43, fig. 2; Pl. 34, fig. 1; Pl. 42, fig. 1). On none of these is the appendage complete. The sympod consists of two joints. The basal joint is short and wide with a ventral medial sharp lobe which obscures the relationship of the next segment. This relationship is shown by PY 20022 (Pl. 42, fig. 1). Only a rectangular free portion of the second segment, to which is articulated a flattened, squamate exopod, is visible on most specimens. Articulated to the mesad base of the second segment is an endopod consisting of three segments and a long flagellum. The exopod (PY 19988, Pl. 33, fig. 1) has a straight lateral edge which is reinforced by a ridge that terminates in a spine. The shape of the antennal scale is best seen in PY 19930 and PY 19948. The main body of the scale is a flat inner lobe which bears a marginal row of setae (PY 19929, Pl. 43, fig. 1). The basal segments of the endopod are robust and of about equal length. The flagellum is about the length of the body. In PY 18856, which is 22 mm. long, the flagellum is 19 mm. in length. The basal annulus of the flagella of the first and second antennae is significantly larger than those succeeding.

The ventral skeletal structure of the head posterior to the mouth

is poorly known. Two small lobelike structures that may be fortuitous scraps or true paragnaths were discovered on the counterpart of USNM 38842-200.¹¹ They are of an acceptable shape, are correctly situated, and arise from a small skeletal element posterior to the mouth.

The body of the left mandible is remarkably well preserved on PY 19931 (Pl. 40, fig. 1). The biting processes are unknown except that the incisor lobe was serrate as seen in PY 19936 (Pl. 42, fig. 2). The three small joints present on some specimens, *e.g.*, PY 19929 (Pl. 43, fig. 1), in the position of a mandibular palp, are the terminal portions of the first maxillipeds. The structure of the mandibular palp is unknown.

A most unusual feature of the mandible of these Crustacea with biramous thoracic appendages is the articulation with the epistome as seen on PY 19931 (Text Pl. 3, fig. c). This well-developed articulation lateral to the labrum is secondary and is characteristic of decapods.

Among the jumble of remains on the fossils of structures which originally supported the mandibles posteriorly, one can sometimes imagine that maxillae can be seen. Under close scrutiny the decipherable structures always prove to be remains of the maxillipeds. If maxillae were present, they would be obscured from view by the large endites of these thoracic appendages. The structures on fossils of *Tealliocaris* interpreted as maxillae by Peach (1908, pl. 1, fig. 7 a) (Text Pl. 7, fig. c) need to be critically re-examined.

The thorax is covered dorsally and laterally by the carapace. Though the carapace and thorax were probably not adnate, nothing is known of the tergites of the eight somites forming this tagma. Between the pleural development of the carapace and the body, branchial chambers were present. Nothing is known of the gills.

The sternites and their corresponding pairs of biramous appendages are well preserved on some of the specimens. The eight sclerites of the sternum are shown by USNM 38843 (Pl. 39, fig. 1). The sternites were sclerosed more than the other skeletal parts. The first thoracic sternite appears to be a small triangular sclerite with a pronounced medial ridge. This is not the complete structure but a reinforced portion between foramina for the legs, *vide* PY 19936

(Pl. 37, fig. 1); its complete shape is transverse with bridges anterior and posterior to each foramen. The seven succeeding sclerites have a central heavily sclerotized portion in bold relief. The raised portion of each sternite is quadrilateral with acute postero-lateral angles. The anterior sternites have a raised medial keel. The sternites become progressively wider placing the foramina for the legs farther apart. The foramina for the legs are surrounded by the marginal recessed portion of the sternites (PY 19936, Pl. 37, fig. 1). Thoracic somites are subequal in length as shown by the sternites. Each sternite is reinforced anteriorly and posteriorly by infolded edges at the intersegmental suture. The sternal sclerites of some of the specimens have been pulled apart suggesting a membranous articulation, see PY 19947 and PY 19971 (Pl. 40, fig. 3; Pl. 36, fig. 2). The thoracic somites were not fused and there was no endophragmal skeleton.

There are two variations of the eighth sternite. On PY 20022 (Pl. 42, fig. 1) this sclerite is not unlike the seventh except for its greater length and convex posterior. At least one-half of the specimens with this skeletal part preserved have an enlarged medial pouch (PY 19947, Pl. 40, fig. 3; USNM 38843, Pl. 39, fig. 1). This structure, which originally was nearly circular, has a large aperture facing slightly to the posterior. The structure is reminiscent of the sperm receptacle of the syncarids and eryonid decapods. The annulus ventralis of other decapods, when present, is on the seventh sternite of the females. The structure must be a sperm receptacle. It is too small for an egg pouch. Though male gonopores are associated with the eighth somite in Eumalacostraca, this is an unlikely male organ.

Evidence of other sexual characters were sought in vain. Female gonopores did not open on the sternite of the fifth somite as there is no trace of them on the many excellent specimens which show this sclerite. It must be assumed that the female gonopores opened on the sympod of the fifth pair of thoracic appendages and the male gonopores on the sympod of the eighth pair of appendages as in Recent decapods.

Eight pairs of thoracic appendages are present on PY 20022 (Pl. 42, fig. 1) and USNM 38843 (Pl. 39, fig. 1). The first two pairs are differentiated as maxillipeds, the third is incipiently modified, and the last five pairs are long, slender pereopods, vide PY

19993 (Pl. 34, fig. 1), PY 20005 (Pl. 34, fig. 2), PY 19953 (Pl. 38, fig. 2), and PY 19988 (Pl. 33, fig. 1).

On several of the specimens parts of the first two pairs of appendages are present. They must be interpreted with caution to avoid misapprehension as it is not always obvious they originate from the first two thoracic somites. It is also unknown to what degree the maxillae had degenerated to foliaceous lobes. Especially confusing are the large lobate endites which arise from the sympod of the maxillipeds and embrace the gnathic structures as on USNM 38843 (Pl. 39, fig. 1). At first it was believed the lobes and segments of appendages shown by PY 19929 (Pl. 43, fig. 1), PY 19988 (Pl. 43, fig. 2), PY 19960 (Pl. 41, fig. 2), and PY 19971 (Pl. 36, fig. 2) were maxillae, but in all cases, the morphology of these parts conforms to the known structure of the first two pairs of thoracic appendages.

The maxillipeds of *A. gracilis* are most unusual. The sympod consists of a single joint. From the mesad side a simple large endite arises. The endite on the first appendage is produced into a blade-like lobe which is twice the size of that of the second; otherwise, the two maxillipeds are similar. Only four joints make up the endopod. They are shown in the restoration (Text Pl. 2). Exopods which may be associated with these appendages can barely be detected on the right side of MCZ 5229 (Pl. 41, fig. 1).

Except for the smaller size of the appendages of the third thoracic somite, the remaining six pairs of endopods are similar. There is a distinct specialization for only the posterior five pairs to function as pereopods. This tendency toward becoming a decapod is apparent in many specimens, vide PY 19953 (Pl. 38, fig. 2) and PY 20005 (Pl. 34, fig. 2).

The two rami of the thoracic leg arise from a short stout sympod. A precoxa cannot be fused into the pleura associated with each appendage as Hansen (1925, p. 138) has claimed is the case with decapods. The simple, unmodified foramina for the thoracic legs have been discussed and illustrated. Only one joint can be distinguished in the sympod of *A. gracilis*. The single large joint is produced mesad and forward into small endites. These are particularly well shown by USNM 38843 (Pl. 39, fig. 1).

The endopod conforms to the basic structure of the malacostracan leg. It has five joints, an ischium, merus, carpus, propodus, and terminal dactylus. The "knee" is between the merus and the carpus. For the proportional development of these joints see the photograph of PY 19953 (Pl. 38, fig. 3) and the restoration.

The exopods are always poorly preserved, but fragmentary evidence of their existence is found on many specimens. Remains of the annulate flagellum are unmistakable. The setiferous annulate portion of the exopod is particularly well preserved on PY 19979 (Pl. 39, fig. 2). The flagellum and the basal unjointed stalk of the exopod are both present on the fourth thoracic appendages of PY 20022 (Pl. 42, fig. 1).

Except by analogy, only the digestive tract is known of the internal anatomy. The gut of many of the specimens has been filled with detrital sediment of the same general nature as the entombing matrix. As shown by PY 19998 (Pl. 35, fig. 4) there is an expansion of the gastric region in the cephalothorax to form a simple undivided stomach. The posterior intestine is a simple tube which terminates on the ventral side of the telson as shown by PY 19993 (Pl. 34, fig. 1).

The abdomens of most of the specimens are preserved in a dorso-ventral position and are extended, but a few have their abdomens reflexed. A gentle flexure as shown by the specimens preserved on their sides (*vide* Pl. 34, fig. 2; Pl. 35, figs. 3, 4; Pl. 38, fig. 2) seems to be normal.

The tergites of the second to fifth abdominal somites are similar except for a slight decrease in size posteriorly. This can be seen in the photograph of PY 19993 (Pl. 34, fig. 1) and PY 19928 (Pl. 35, fig. 3). The first tergite is never well preserved (PY 19983, Pl. 35, fig. 2). If it were not for the sternites, there would be no conclusive proof of its existence on the specimens of *A. gracilis* studied. The tergites are highly arched as shown by PY 19996 (Pl. 36, fig. 1). Ventrally they are produced into pleural lobes with an acutely pointed apex (PY 19931, Pl. 39, fig. 3). The tergite of the sixth abdominal somite is distinguished only by the marginal modification of the pleural plate and the postero-lateral margins to accommodate the uropods.

Sternites of the first five abdominal somites are narrow sclerotized bars which are expanded near their juncture with the tergites where there are foramina for the swimmerets. These structures are shown by USNM 38843 (Pl. 39, fig. 1) and MCZ 5229 (Pl. 41, fig. 1). The ventral membranous surface of the abdomen between the sternites is partially preserved on USNM 38843. The appendages of the first five abdominal somites are unknown, but from their foramina (Pl. 42, fig. 1) they must have been small swimmerets.

The appendages of the sixth abdominal somite are large uropods. These contribute to the formation of a caudal fan. As shown by PY 19932 (Pl. 31, fig. 1), PY 19993 (Pl. 34, fig. 1) and PY 19996 (Pl. 36, fig. 1) these appendages have a large, one-jointed sympod, a bladelike exopod, and a lobate endopod. The outer margin of the exopod is strongly sclerotized and is produced into a spine. This marginal spine extends beyond the position of the oblique suture that separates the lobe of the blade into two unequal parts. The true shape of the endopod as a simple lobe can be seen only on the ventral counterpart of PY 19932 (Pl. 31, fig. 2). Marginal setae are remarkably well preserved on nearly all of the specimens figured. No evidence of statocysts or other sensory organs in the uropods is present.

The flattened body of the telson is more or less pentagonal. From its broad base, the lateral margins flare slightly and terminate in small spines. Small furcal lobes arise inward to the lateral spines. Two additional pairs of small spines are present inward to the furcal lobes on the postero-lateral margins. The inward pair are marginal to the articulation of the medial spine. A similar fixed spine is present on the telson in the sagittal plane and projects over the articulation. The shape and proportion of these features are displayed by PY 19996 (Pl. 36, fig. 1) and PY 19932 (Pl. 31, fig. 1). Situated mid-ventrally on the body of the telson is the anus.

Synopsis.—A new monotypic genus, *Anthracaris*, is established for a pygocephalomorph crustacean with a broad applanated carapace distinguished by having a pair of hepatic spines. The most significant differences from *Pygocephalus* are the absence of oostegites and the shape of the sympods of the thoracic appendages. Though the thoracic legs are biramous and their sympods consist of only one

joint, this crustacean displays many characteristics of the eryonid decapods. There is a secondary articulation between the mandible and the epistome, the endopods of the first two pairs of thoracic legs are modified as maxillipeds, and the third is incipiently modified. There is a seminal receptacle on the eighth sternite of the females. The genus has retained the primitive furcal lobes and median spine on the telson. Specific criteria of *A. gracilis* are the characteristics of the specimens described.

Stratigraphic occurrence.—Francis Creek shale, Carbondale formation, Alleghany series (Westphalian), Pennsylvanian in Mazon Creek nodules.

Localities.—Grundy and Will counties, Illinois.

Collections.—The best collection is the S.S. Strong collection at Yale University. Other collections are in the Chicago Museum of Natural History, Illinois State Museum of Natural History, University of Illinois, Illinois Geological Survey, U.S. National Museum, and the Museum of Comparative Zoology.

Holotype.—ISMNH 3067 in the collection of the Illinois Geological Survey is the holotype. Y-343 in the collection of the University of Illinois is mislabelled. The plesiotypes studied by Packard are catalogued as No. 38843 in the collection of the U.S. National Museum.

Genus **MAMAYOCARIS**, new genus

A single compressed specimen of a pygocephalomorph was discovered in 1956 by S. H. Mamay of the U.S. Geological Survey in the Vale formation of Permian age south of Abilene, Texas. Its superficial appearance and the marginal branchiostegal serrations of the carapace are characteristics it possesses in common with species of *Anthracaris* and *Pygocephalus*. Through the courtesy of Donald Baird of Princeton University, a large number of specimens, some with better carapaces, representing the same species were brought to my attention. They are from the Opeche formation of Permian age near Rapid City, South Dakota. From these specimens it was determined that the new species differs in several significant characteristics from the known Pennsylvanian and Permian genera.

The only Permian pygocephalomorphs previously known were

Notocaris Broom (1931) from South Africa and *Paulocaris* Clarke (1920) (= *Pygaspis* Beurlen, 1934, and *Liocaris* Beurlen, 1931) from Brazil. Hitherto, pygocephalomorphs have not been reported from strata younger than Westphalian, Middle Pennsylvanian, in the Northern Hemisphere. The new genus is named *Mamayocaris* in recognition of the important paleontological discovery of S. H. Mamay.

Paulocaris has the mid-dorsal carina on the carapace developed into a short prominent crest. The carina is unknown on *Notocaris* and is subdued to the point of being almost undetectable on *Mamayocaris*. The extended compressed carapaces of *Paulocaris* have a greater width than length. On *Mamayocaris* the length and width are approximately equal, whereas on *Notocaris* the width is less than the length. Both southern hemispheric genera differ from *Mamayocaris* by having the abdomen reduced and flexed under the cephalothorax in a crablike manner.

The new genus has its closest phylogenetic relationships with *Pygocephalus* and *Anthracaris*. It (Text Pl. 5) is distinguished by the absence of a pair of hepatic spines, indistinctness of the mid-dorsal carina, shortness of the antero-lateral spines and the more posterior course of the cervical groove on the carapace. The cornea of the stalked compound eyes is abnormally large and the shape of the telson is subtriangular. The seminal receptacle and marsupium on the females are not known. The endopods of the thoracic legs display a decapodous tendency for reduction of the first three pairs to maxillipeds as on *Anthracaris*. The symopods of these legs are more like those of *Anthracaris* than *Pygocephalus*.

The genus is monotypic, represented only by *Mamayocaris jepseni*.

***Mamayocaris jepseni*, new species**

Pl. 44, figs. 1-3; Pl. 45, fig. 5;
Text Pl. 5

This species is characterized by the shortness of the antero-lateral spines, smoothness of the carapace, and existence of only five inconspicuous serrations on the anterior portion of the branchio-stegal keels. The individuals of this species are comparatively small. Of the 47 specimens on which measurements of the carapace could

be made, the largest was 10.2 mm. in length and the smallest was 7.5 mm. The mode and median were 8.5 mm.

Description of the specimens.—The holotype, USNM 133393 (Pl. 44, figs. 1-3), is preserved as a carbonized compression of low relief in a light-gray siliceous mudstone. The details of the dorsal surface of the carapace cannot be seen, but otherwise the specimen is remarkable for the many morphological features of the body and appendages preserved.

The length of the body of the holotype, telson spine not included, is 19.0 mm. and the length of the carapace is 9.7 mm. Thus, about fifty percent of the length of the animal's body was covered by the carapace. On the paratypes from South Dakota the ratio is fifty to fifty-one percent and the carapace length to width ratio is 0.9 to 1.0.

Remains of about 164 individuals on a slab of limestone and four on pieces of fine red sandstone are paratypes. The limestone is thinly laminated. The more nearly pure calcite layers are light tan in color, but because of the many layers of red, detrital partings, the rock appears reddish-brown. The specimens are all dorso-ventral compressions of low relief. Both dorsal and ventral surfaces and impressions of these surfaces are present. Except for the natural impression of the dorsal features of the carapace, the preservation is extremely poor. However, two specimens do reveal characteristics of the telson that would otherwise remain unknown. No residue of the original organic skeletal material remains. The form of the compressed exoskeletons has been duplicated with an earthy calcite. Few of the specimens are of complete animals.

Features of the carapace can be seen on several of the paratypes, *e.g.*, PU 83463 a (Pl. 45, fig. 5). They have the same small antero-lateral spines and the five small inconspicuous serrations of the branchiostegal keel as the holotype (Pl. 44, fig. 3). The surface of the carapace is smooth. A dorsal carina is conspicuous on all pygocephalomorphs from the Pennsylvanian. In this species it is barely detectable. There is a pair of gastric spines, but there are no hepatic spines. Only the base of the rostrum was seen. On the many specimens with this feature, none was complete. The course of the cervical groove on the carapace is more posteriorly oriented than

on any other Upper Paleozoic crustacean. Near the mid-dorsum, where it diminishes and terminates, each lateral sulcus is directed toward the posterior.

As far as known, the body and appendages have the same structural plan as *Anthracaris*. It is only on the holotype that their morphology is decipherable (Pl. 44, figs. 2, 3).

Eyes and portions of both pairs of antennae are the only features of the head exposed. The first antenna is believed to be like that of *A. gracilis*. The scape of the scale, a process of the second joint of the sympod of the second antenna, has its distal end transversely oblique to the outer margin. Whereas the absence of the blade of the squama is a feature of preservation, this is not. The flagellum of the second antenna is nearly as long as the animal.

The left eye on this fossil is the best preserved stalked compound eye known on Paleozoic caridoid fossils. The faceted cornea forms a large hemisphere (Pl. 44, fig. 3). The juncture with the stalk is straight.

Except for lacking the mid-ventral longitudinal ridge on the thoracic sternites, the eight sclerites are not distinctive. Absence of a medial keel is not due to preservation as the sternites can be studied both as compressions and external impressions (Pl. 44, figs. 2, 3). The paratypes also have no keel. On none of the specimens is there evidence of a seminal receptacle on the eighth sternite.

The last five thoracic appendages are beautifully preserved on the right side of the holotype. The basal shaft and the annulate flagellum of the exopod are present on both counterparts of the fourth thoracic appendage. A flagellum just forward of this is present on one counterpart (Pl. 44, fig. 2). This must have had its origin on the third appendage. Joints of the endopods of the five pereopods are remarkably well preserved; however, the small dactylus is present only on the seventh leg (Pl. 44, fig. 2). The "knee" portion of the third thoracic appendage can be seen. As in *A. gracilis*, this endopod is smaller than those of the succeeding appendages. Because the other appendages are identical to those of *A. gracilis*, it is assumed the third pair of endopods were incipiently modified as maxillipeds.

The Texas specimen is the only pygocephalomorph fossil with the tergite of the first abdominal somite well displayed. The sclero-

tized part is less than half the length of the typical abdominal tergites. It can be seen in the photographs of counterpart a (Pl. 44, figs. 1, 3). The apex of the pleural lobes of the tergites of abdominal somites two to five are sharper than on *A. gracilis*, and the anteroventral margins are straight. The tergite of the sixth abdominal somite is not well preserved; neither are the telson and uropods of the caudal fan. What can be seen of the telson on this specimen is not distinctive; however, on paratype PU 83463 a (Pl. 45, fig. 5), the telson is subtriangular with the furcal lobes articulated closer to its base than on *A. gracilis*. The rami of the uropods and the furcal lobes are fringed with setae. There is a broad triangular spine articulated medially on the telson.

Synopsis.—*Mamayocaris jepseni* is the only pygocephalomorph crustacean known from Permian deposits of the Northern Hemisphere. *Notocaris tapscotti* (Woods) (Woods, 1923, Broom, 1931) from the Upper Dwyka shales of Kimberly, South Africa, and *Paulocaris pachecoi* Clarke (1920) from the Iraty shales of Brazil are the only other Permian species known. *Pygaspis brasiliensis* Beurlen, *P. quadrata* Beurlen (1934) and *Liocaris huenei* Beurlen (1931) from the same deposits as *Paulocaris* are believed to be synonyms. The genera from the Southern Hemisphere differ from *Mamayocaris* by having the abdomen slightly reduced and flexed under the cephalothorax. The new genus is closely related to *Anthracaris* but is readily distinguished by the absence of hepatic spines, indistinct dorsal carina, and the more posterior course of the cervical groove. The hemispherical cornea of the compound stalked eyes is abnormally large. The appendages are similar in structure to those of *Anthracaris*. It is unknown if seminal receptacles or oostegites exist on the females. The telson is subtriangular with the furcal lobes being articulated nearer the base of the telson than they are on *Anthracaris*. The species is characterized by its small size and by five inconspicuous branchiostegal serrations.

Stratigraphic occurrence.—Holotype is from the Vale formation, Clear Fork group, Leonardian series, Permian System. It was associated with remains of terrestrial plants, palaeoniscoid fish, amphibians and reptiles. The only other invertebrates are rare estherian fossils. The stratigraphy and paleoecological condition of this de-

posit have been summarized by Wilson (1953). The paratypes from the contemporaneous Opeche formation were found in association with palaeoniscoid fishes in a lagoonal deposit.

Collections.—The holotype, USNM 133393, was collected by S. H. Mamay in a quarry six miles southwest of Lawn, Texas, on the property of C. O. Patterson in the southern part of Taylor County, S.W. 1/4 of S. 436 of the M.P. King survey. The 168 paratypes, PU 83463, were collected by G. L. Jepsen with financial support from the Scott Fund, Princeton University. They are from the State Cement Quarry, three miles west of Rapid City, South Dakota.

Types.—The holotype is No. 133393 in the collection of the U.S. National Museum. There are 168 paratypes catalogued as No. 83463 in the collection of Princeton University. The better specimens have been assigned alphabetical suffixes, a to k.

Genus **PYGOCEPHALUS** Huxley, 1857

The name of this genus is indicative of the difficulty Huxley had in interpreting the three original specimens which presented the ventral skeletal structure of this crustacean. Outlines of the carapace were not present. All that he had to work with were the thoracic sternities, the cephalic and thoracic appendages; and on all specimens the abdomens were reflexed upon themselves. Upon deciding the end with the flagella was anterior, he noticed the similarities of the structures present to those of the Recent *Mysis*. It is unfortunate that *Pygocephalus* has been restricted to fossils that present only the ventral skeleton. There is no question but that *Anthrapalaemon* Salter (1861) with a carapace is the dorsal surface of the same species and that *Necroscilla* Woodward (1879) is a poorly preserved abdomen.

Woodward (1907 b) was the first to note the many common characteristics observed on specimens referred to both *Anthrapalaemon* and *Pygocephalus*, but he failed to realize the taxonomic significance. Other authors (Peach, 1908, p. 37, Copeland, 1957 b, p. 43) noted the close generic association and Beurlen (1930, p. 126) suggested they should be synonymized. When it is obvious that these two genera are different parts of the same animal, perpetuation of their use is absurd. *Anthrapalaemon* Salter, 1861, must

be suppressed as a junior synonym of *Pygocephalus* Huxley, 1857. The type species is *P. cooperi* Huxley.

Pygocephalus (Text Pl. 6) is distinguished by the absence of a pair of hepatic spines on the carapace and massive development of the sympods of the first two thoracic appendages. It is believed that the females had six or seven pairs of oostegites and a seminal receptacle on the eighth sternite.

***Pygocephalus dubius* (Milne-Edwards), 1840** Pl. 38, fig. 1; Text Pl. 6

- Apus dubius* Milne-Edwards, 1840, in Prestwich, p. 491, pl. 41, fig. 9.
Pygocephalus cooperi Huxley, 1857, p. 363, pl. 13, figs. 1, 3.
Anthrappalaemon grossarti Salter, 1861, p. 530, text figs. 1-4.
Anthrappalaemon (Palaeocarabus) dubius, Salter, 1861, p. 532, figs. 6, 7 a, 7 b.
Palaeocarabus russellianus Salter, 1863 b, p. 520, figs. 1, 2.
Anthrappalaemon (Palaeocarabus) hilliana Dawson, 1877, p. 56-57, fig. 1.
Anthrappalaemon (Palaeocarabus) hillianum, Dawson, 1878, Appendix, p. 55, fig. 10.
Necrosilla wilsoni Woodward, 1879, p. 551-552, pl. 26, fig. 3.
Anthrappalaemon parkeri Woodward, 1907 a, p. 568.
Pygocephalus cooperi, Woodward, 1907 b, p. 400-406, figs. 1, 2, pl. 18, figs. 1-6.
Pygocephalus (Anthrappalaemon?) parkeri, Woodward, 1907 b, p. 406-407, fig. 2.
Anthrappalaemon russellianus, Peach, 1908, p. 29-39, pl. 4, figs. 1-7.
Anthrappalaemon hillianus, Bell, 1922, p. 162, pl. 1, fig. 10.
Pygocephalus cooperi, Beurlen, 1930, p. 442, fig. 61.
Anthrappalaemon dubius, Van der Heide, 1951, p. 26-37, pl. 3, figs. 4, 5, pl. 4, figs. 2-10, pl. 5, figs. 1-10, pl. 6, figs. 1-5.
Anthrappalaemon dubius, Rhodes and Wilson, 1957, p. 1159-1165, text figs. 1, 2.
Anthrappalaemon dubius, Copeland, 1957 b, p. 42, pl. 10, figs. 3-6, pl. 11, figs. 2, 3.
Anthrappalaemon sp. Copeland, 1957 b, p. 43, pl. 21, fig. 2.
Pygocephalus cooperi, Copeland, 1957 b, p. 43, 44, pl. 10, fig. 1, pl. 11, fig. 1.
Pygocephalus cf. *cooperi*, Copeland, 1957 b, p. 44, pl. 10, fig. 2.

The systematics of the many species that have been referred to *Anthrappalaemon* and *Pygocephalus* needs critical review. However, for the present we must rely on the work of Van der Heide (1951) and Rhodes and Wilson (1957) on the European carapaces referred to *Anthrappalaemon*. They synonymized all of the European species and *Anthrappalaemon hillianus* Dawson from Nova Scotia. Peach (1908, p. 31) called attention to variations in the number of marginal serrations as a product of preservation; thus, the serra-

tions are not a reliable specific criterion. This and the variations in distribution and density of the tuberculate ornamentation of the carapaces preserved as impressions in black shale are unreliable bases for differentiating species. Rhodes and Wilson (1957, p. 1161-1164) attempted to prove by a statistical analysis of the size frequency and other parameters of the British specimens that only one species should be recognized.

The systematics of *Pygocephalus dubius* is further complicated by the paleontological practice of recognizing form genera. *Necroscilla* Woodward, 1879, is an abdomen. *Anthrapalaemon* Salter, 1861, has been used for those Crustacea showing the dorsum, particularly the carapace. On the other hand, *Pygocephalus* Huxley, 1857, has been used for classification of remains presenting the ventral aspect of the exoskeleton. Species assigned to these genera have been defined on different distinguishing characteristics. In the proven absence of reliable differences, there is no recourse but to synonymize at this time. The synonymy presented above includes only those taxonomic contributions relative to the classification of the Canadian fossils. More complete synonymies can be found in the works of Van Straelen (1931, p. 23-26, p. 32-35), Van der Heide (1951) and Rhodes and Wilson (1957).

Morphology.—The morphological description presented below is not restricted to the specimens examined. For many details I have had to rely upon published illustrations of specimens of *Anthrapalaemon* and *Pygocephalus*. The only previous studies worthy of note are those of Woodward (1907 b, *Pygocephalus cooperi*) and Peach (1908, *Anthrapalaemon russellianus*). A composite restoration of *Pygocephalus dubius* is presented in Text Plate 6. Features shown by discontinuous line have not been seen in this study. Their authenticity is supported in the literature cited.

There are many variations due to preservation of the fossils. The figures of the carapace drawn by Rhodes and Wilson (1957, text fig. 2) and reproduced herein (Text Pl. 6, figs. b, c) are incorrect in several respects because they failed to differentiate original features from those produced by fossilization. The "raised central area" is a compressional reflection of the thorax, particularly that of the sternal skeleton. They also believed the cervical groove gave

rise to anterior and posterior branches which separated lateral margins of the carapace. As in *Anthracaris*, this is not an original feature (compare photographs of GSC 12813, Copeland, 1957 b, pl. 10, fig. 4, to that of GSC 12821, pl. 10, fig. 6).

The dorsal characteristics of the carapace of *Pygocephalus dubius* from the Canadian deposits are well preserved on GSC 12821 (Copeland, 1957 b, pl. 10, fig. 6). The compressions are spread laterally such that they are as wide as long (GSC 12821 is 18 mm. long). Measurements on the nine specimens in the MCZ collection on which the length could reliably be made ranged from 7 to 17 mm. The mode is 12 mm. The lateral margins of the carapace are broadly curved. As Peach has noted this is a branchiostegal keel and not the true ventral edges of the carapace. The marginal keels are armed with serrations. They are conspicuous anteriorly; some European specimens have denticles of equal size along the complete length of both edges. The antero-lateral angles of the carapace are produced as spines. Inward from the spines, the anterior margin is not so deeply recessed as in *Anthracaris*. Though most drawings of this species show a short rostrum, it is nearly one-half the carapace length on GSC 12821. A prominent mid-dorsal carina extends forward from the posterior margin for two-thirds the length of the carapace to the cervical groove. The groove does not cross the mid-dorsum. Each lateral branch arises lateral to the termination of the carina. A pair of ridges on the gastric area of the carapace gives rise to spines which project anteriorly. No eminences of any sort are present in the hepatic region. Relative preservation of the tubercular ornament is evident, but there may have been considerable original variation. The better preserved European specimens often have the carapace completely covered with strong tubercles (*vide, Anthrapalaemon russellianus*, Peach, 1908, pl. 4, fig. 1), but on the Canadian fossils the tubercles are subdued with the larger papillae just posterior to the cervical groove and scattered posteriorly on either side of the dorsal part of the carapace.

The ventral aspect of the cephalon is poorly known. Copeland (1957 b) has figured specimens from Canada identified as *Pygocephalus cooperi* (GSC 12811, pl. 10, fig. 1; GSC 12810, pl. 10, fig. 2; GSC 12858, pl. 11, fig. 1). Though extremely poorly preserved,

it is probable that these specimens are of the same species as those from England and Scotland. As shown by Woodward (1907 b) and Peach (1908), the two pairs of antennae do not differ from those of *Anthracaris gracilis*. The sympod, including the stipe for the exopodal scale, and the basal joint of the endopod of the second antennae can be seen on MCZ 6718 (Pl. 38, fig. 1). Peach's (1908, p. 34, pl. 4, fig. 2, 3) notation of large stalked compound eyes is of doubtful authenticity. Except for a plate on MCZ 6718 that may be a portion of the labrum, no other features of the head are known.

The description of the ventral structures of the thorax that follows is based largely on MCZ 6718 (Pl. 38, fig. 1) from the Upper Carboniferous of England. The sympods of the first pair of thoracic appendages are produced as large, massive rounded lobes and extend forward. The ischium and merus of the endopod can be seen arising laterally. Though shortened, these joints are no less robust than those of the succeeding pereopods. The sympods of the second pair of thoracic appendages extend to the mid-ventral line and though massive, lack the anterior extensions of the preceding pair. The endopod of these appendages appears to differ in no respect from the typical pereopod. All five joints of this ramus can be distinguished. The basal stalk and flagellum of the exopod can be seen arising from the sympod of the fifth appendage. Woodward observed seven similar biramous pereopods on the specimens he figured (1907 b, pl. 18, figs. 1, 4).

The sympods of thoracic appendages three to eight are subquadrate in shape. The peculiar anterior shoulder may have been for the support of oostegites.

Only seven sternites are evident on the Canadian and British specimens. If present, the sternal sclerite of the first thoracic somite was reduced as on *Anthracaris*. It is obscured on all specimens by the massive sympods of the first and second pairs of appendages. The last sternite of MCZ 6718 is badly deformed, but is larger and has a transverse bulge. It lacks a seminal receptacle. Woodward (1907 b, pl. 18) called attention to sexual differences in a specimen of *Pygocephalus*. The specimens like that of MCZ 6718 he correctly interpreted as males. He showed that some specimens have six or seven large platelike imbricating endites, oostegites, to form a

marsupium. That the oostegites are not always preserved on the females is proven by the specimen figured by Woodward on plate 18, figure 3. The sternites of this specimen are not covered by the marsupium, but it is evidently a female as the last sternite has a large circular pouch clearly figured. It is comparable to the seminal receptacle on specimens of *Anthracaris gracilis*. Woodward misinterpreted this as a "doubtful (anal?) plate displaced." The poorly preserved remains designated as male genital papillae by Peach (1908, pl. 4, fig. 2) must also be relics of such a chamber.

The presence of a seminal receptacle on the last thoracic sternite is most peculiar in that Woodward (1907 b, pl. 18, figs. 3, 5) has proven the females to have oostegites forming a marsupium. These are characteristics that previously were believed to be mutually exclusive. The seminal receptacle is a feature of syncarids and decapods whereas oostegites are restricted to the peracarids.

The gills mentioned and figured by Peach (1908, p. 35, pl. 4, figs. 3, 4) are of doubtful authenticity.

The dorsum of a poorly preserved abdomen from Canada has been figured by Copeland (GSC 12812, 1957 b, pl. 10, fig. 5). Superior specimens are figured by Woodward (1907 b) and Peach (1908). The abdomen is about the same length as the cephalothorax. Only five tergites, a pair of uropods and the telson have been figured. As in *Anthracaris*, the first abdominal tergite must have been reduced as it has not been observed. Furcal lobes are present on the telson. The median spine has a broad base, but narrows rapidly and is sharply pointed.

It is believed that *Amphipeltus paradoxus* Salter (1863 a, p. 75) and *Diplostylus dawsoni* Salter (1863 a, p. 76) may also be synonyms of this species. They will be discussed later.

Synopsis.—The recognition of three form genera for the dorsal and ventral side of the same species and its abdomen is an indefensible paleontological practice; therefore, *Anthrapalaemon* and *Necroscilla* are suppressed as synonyms of *Pygocephalus*. Valid criteria remain to be presented for distinguishing the many species previously assigned to these genera. Thus *Anthrapalaemon hillianus* Dawson from the Maritime Provinces of Canada is best classified at this time as *Pygocephalus dubius* (Milne-Edwards). Further

study will probably prove it to be worthy of recognition as a subspecies.

The genus is distinguished from *Anthracaris* by the absence of a pair of hepatic spines on the carapace, and by the massive development of the sympods of the first two thoracic appendages. The females had six or seven pairs of oostegites forming a marsupium. It is proven that the females of both genera had large seminal receptacles on the sternite of the eighth thoracic somite.

Stratigraphic occurrence.—Westphalian, Pennsylvanian. Copeland reports specimens from the Riversdale, Cumberland and Pictou groups in Nova Scotia.

Localities.—England, Scotland, Netherlands, Belgium, France, Nova Scotia, and United States(?). For the many localities in Canada that these fossils have been collected, see Copeland (1957 b, p. 42-44). (Note: A single poorly preserved specimen (MCZ 5322) of the sternum of a pygocephalomorph was collected by Donald Baird from below the upper Freeport coal, Alleghany series at the Linton mine dump near the mouth of Yellow Creek, Jefferson County, Ohio. In that it lacks a median keel, it is probably *Pygocephalus* rather than *Anthracaris*.)

Collections.—The best collections of American specimens are in the museum of the Geological Survey of Canada, Ottawa, Museum of Comparative Zoology, Harvard University, and the Department of Geology at Princeton University.

Type.—The holotype of *Apus dubius* Milne-Edwards is No. 54398 in the collection of the Geological Survey Museum, London, England. The repository of Dawson's type for *Anthrapalaemon hillianus* is unknown.

Genus **PSEUDOTEALLIOCARIS**, new genus

Because the carapaces of some poorly preserved Pennsylvanian fossils from Nova Scotia have a median and two pairs of lateral carinae they were assigned by Copeland (1957 b, p. 44-47) to the genus *Tealliocaris*, a pygocephalomorph genus known only from Mississippian strata of Scotland (Peach, 1908, p. 9-27) and France (Carpentier, 1913, p. 344-345). The carapaces of the specimens from

Canada are produced laterally by the development of large branchiostegal keels, and there are long pointed antero-lateral spines. These are characteristic features of the other Pennsylvanian genera and not *Tealliocaris*. In common with *Tealliocaris*, the new genus has carinae on the carapace and the abdominal tergites, a small embossed area at the base of the rostrum, and a subtriangular telson. Furcal lobes and a median spine are present on the telson of *Pseudotealliocaris*. However, the thoracic sterna are devoid of sternal processes. A drawing of the carapace of *Pseudotealliocaris* and a restoration portraying the known morphological features of *Tealliocaris* are presented in Text Plate 7. The type species is *Tealliocaris caudafimbriata* Copeland (1957 b, p. 44).

***Pseudotealliocaris caudafimbriata* (Copeland), 1957** Text Pl. 7, fig. b

Tealliocaris caudafimbriata Copeland, 1957 b, p. 44, pl. 12, fig. 3.

Tealliocaris barathrota Copeland, 1957 b, p. 45-46, pl. 13, figs. 2-6, pl. 14, figs. 2, 3, 1 text fig.

Tealliocaris belli Copeland, 1957 b, p. 46-47, pl. 12, fig. 4.

Anthracophausia sp. Copeland, 1957 b, p. 47, pl. 14, fig. 1.

Copeland (1957 b) used such characteristics in his specific diagnosis of the three species named as "a distinct posterior swing of the thoracic shield and in lacking crenulations interior to the carapace ridges," "Carapace shield-shaped, strongly wrinkled and pitted with seven well-developed dorsal keels," and "having large, wrinkled first uropods and is much larger in size." Fossils of animals with chitinous exoskeletons always present great noninnate variations such as these due to deformation and varying retention of skeletal parts, particularly when they are preserved as compressions, carbon films, and impressions in shale.

The length of the holotype of *Tealliocaris caudafimbriata* is 13.5 mm., and the length of the carapace is 6.7 mm. The length given for *T. barathrota* is 16 mm. and for *T. belli* is 26 mm. At this time there is no valid basis for recognition of more than one species in the genus *Pseudotealliocaris*. Its characteristics are those of the specimens figured by Copeland.

Description of the specimens.—I have not had access to the specimens in the Geological Survey of Canada collections that were available to Copeland, but it is apparent from his figures that the

specimens have been badly misinterpreted. It was possible to determine the following characteristics from his photographs.

The carapace covers 46 to 48 percent of the length of the body, telson spine not included. The telson is about one-third the length of the carapace. As preserved, the carapaces have a maximum width only slightly less than the length.

The true ventral edges of the carapace cannot be seen because of pronounced branchiostegal keels as on *Anthracaris*. The margins of these keels are either finely serrate or are granulate (GSC 10384, Copeland, 1957 b, pl. 13, fig. 6), and there is a pair of long, sharp antero-lateral spines. The frontal margin of the carapace has an antennal re-entrant. As far as can be determined, the rostrum was of moderate length. It arises from a parabolically shaped embossed development of the gastric region of the carapace (GSC 10384, *op. cit.*, GSC 12785 c, pl. 13, fig. 4). The peripheral margin of this area has been wrinkled on some of the compressions. This, Copeland 1957 b, p. 45, text fig.) has termed a "gastric fold". A mid-dorsal carina and two lateral pairs of carinae are present posterior to the cervical groove which Copeland (1957 b, p. 44, 45) has misinterpreted as a "cervical fold". The first pair of lateral carinae is developed anterior of the cervical groove as crests. These terminate as gastric spines. The complete dorsal surface is covered by a fine pitting.

The antennae and other appendages of the cephalothorax are too poorly portrayed for interpretation. The sternites of the thoracic tagma are the same shape as on all other pygocephalomorphs. There are no sternal processes (GSC 12785 d, Copeland, 1957 b, pl. 13, fig. 5) as on the species of *Tealliocaris*. No evidence of a seminal receptacle is present on *Pseudotealliocaris*.

The six abdominal tergites are poorly preserved on several specimens. They have one or more longitudinal carinae dorsally on the tergites and their pleural lobes are pointed.

The holotype of *Tealliocaris caudafimbriata* (Copeland, 1957 b, GSC 10382, pl. 12, fig. 3) has retained both rami of the uropods. Each ramus has a strongly sclerotized median ridge from which there is a radiating structure. The specimens referred to *Anthraco-phausia* sp. (Copeland, 1957 b, GSC 12783, pl. 14, fig. 1) show only

the axial structure of the uropod rami. The subtriangular telson is displayed on GSC 12782 (Copeland, 1957 b, pl. 14, fig. 3). Copeland (1957 b, p. 46) referred to "two swimmerettes on each side of the telson behind the uropods." These are the furcal lobes. There are two small fixed spines at the lateral edge of the narrow transverse tip of the body of the telson, between which a median articulated spine must have originated.

Synopsis.—A new genus, *Pseudotealliocaris*, is established for the three Pennsylvanian species from Nova Scotia previously referred to *Tealliocaris*. These pygocephalomorph crustaceans do have longitudinal carinae on the carapace and abdominal tergites and the telson is subtriangular; however, the carapace is produced laterally as branchiostegal keels which terminate anteriorly as long sharp spines. The surface of the carapace of *P. caudafimbriata* is punctate and the marginal keels are either granulate or finely serrate. Two species are suppressed as synonyms.

Stratigraphic occurrence.—Copeland reported specimens from the Casco group, Westphalian, Pennsylvanian.

Localities.—Copeland (1957 b) cited localities near Parrsboro, Mabou River, and Creignish, N.S., Canada.

Collections.—The few specimens that have been discovered are numbers 10381, 10382, 10384, 12782, 12783, 12784 and 12785 a-d in the Museum of the Geological Survey of Canada.

Holotype.—No. 10382 in the collections of the Geological Survey of Canada is the holotype of *Tealliocaris caudafimbriata*.

Genus **ANTHRACOPHAUSIA** Peach, 1908

Anthracophausia dunsiana Peach, 1908, p. 61-67, pl. 9, figs. 1-15.

Anthracophausia traquairi (Peach), Peach, 1908, p. 67-69, pl. 10, figs. 1-5.

Anthracophausia sp. Carpentier, 1913, p. 348, pl. 4, fig. 10.

Anthracophausia, Van Straelen, 1931, p. 23.

The generic name selected for these Upper Paleozoic Crustacea is most appropriate as far as superficial resemblances to the Recent euphausiids are concerned. Peach (1908, p. 62, pl. 9, figs. 2-4) presented reliable evidence that the carapace was not fused with the posterior thoracic segments, but this primitive characteristic is to be expected of the ancestral euphausiids. Most disconcerting, how-

ever, is the presence of a marsupium on the females of the closely related contemporaneous fossil *Crangopsis* (Peach, 1908, p. 74, pl. 11, fig. 14). *Anthracophausia* and *Crangopsis* are distinguished only by the length of their rostra; consequently they both must be classified together but not as genuine members of the Order Euphausiacea.

Anthracophausia is a prawnlike crustacean which is consistently found as lateral compressions. Its chitinous carapace is thin and smooth and is approximately one-third the total length of the animal. A short, spikelike rostrum arises mid-dorsally on the anterior and its base grades imperceptibly into the anterior margin of the carapace. A cervical groove is faintly distinguishable. The margins of the carapace are reinforced by an unusually narrow band. These generic characteristics will be amplified in the morphological discussion.

The type species, *A. dunsiana* Peach (1908, p. 61-67, pl. 9, fig. 11-15), is from the Cementstone group, Tuedian, Mississippian of Scotland. The specimens identified by Copeland (1957, p. 47, pl. 14, fig. 1) as being congeneric are not representatives of this genus. The presence of carinae on the abdominal tergites prove they are specimens of *Pseudotealliocaris caudafimbriata*, a species found at the same collecting locality.

Only two specimens have been collected from Mazon Creek, Illinois; one lacks its counterpart. These fossils portray innate characteristics distinguishing them as representing a new species. It is the first authentic record of this genus from North America and from the Pennsylvanian System.

***Anthracophausia strongi*, new species** Pl. 48, figs. 1-3; Text Pl. 8, fig. f

Though much like the type species, the specimens from Illinois have two distinguishing characteristics. The rostrum is straight and sharply pointed and is easily distinguished from the arched falciform structure of the Scottish species. The pleural lobes of the abdominal tergites narrow to a sharp apex on *A. dunsiana*. They are broadly rounded on the new species.

The average size of *A. dunsiana* is given as 30 to 40 mm. Its associate, *A. traquairi*, is 80 to 100 mm. in total length. Part of

this greater length is due to an unusually long rostrum. The Pennsylvanian species from Illinois is estimated to have been 25 to 30 mm. long. The length from the anterior of the carapace to the base of the telson is 21 mm. on PY 18884 and 20 mm. on PY 18821. Respectively, the measurements of lengths of the following features on these specimens are: rostrum, 2.8 mm. and 2.5 mm.; carapace, 7.7 mm. and 6.5 mm.; sixth abdominal somite, 3 mm. and 2.5 mm.; and the telson of the latter is 4 mm. in length.

Description of the specimens.—The compressions in the Mazon Creek nodules leave much to be desired for morphological interpretation. The chitin has disintegrated and form is discernible only from impressions. Nothing that could not be confirmed on the specimens has been drawn on the restoration (Text Pl. 8, fig. f).

The carapace is a thin, smooth, chitinous shield that wrapped closely around the thorax (PY 18884, Pl. 48, fig. 3, and PY 18821, Pl. 48, figs. 1, 2). A cervical groove is faintly perceptible and extends obliquely downward from a position mid-dorsally about one-third the length of the carapace from its front. There is a faint mid-dorsal keel (PY 18884). The posterior edge is deeply emarginated dorsally and the large lateral lappets on the sides are broadly rounded. The stout, sharply pointed rostrum is reinforced at its base by a low median keel. The lateral flanges grade imperceptibly into the carapace and the orbital notches. The complete marginal edges of the carapace are reinforced by a narrow rim.

Only partial remnants of the antennae and the mandibular palps have been seen. However, the orbital notches of the carapace and the hollowed-out portion of the peduncle of the first antennae substantiate belief in the original existence of a pair of stalked eyes. There can be little doubt that the large compound eyes figured by Peach (1908, pl. 9, figs. 1-4, 10-12) are authentic.

Three joints of the peduncle of one of the first pair of antennae are present on both specimens. The basal joint has its proximal dorsal surface hollowed out comparable to the "eye sockets" in some of the Recent Crustacea. Distad, this joint becomes cylindrical and extends beyond the tip of the rostrum. The second and third are short. Peach (1908, pl. 9, figs. 1, 3) illustrated two short flagella on each of the first antennae of the species he studied.

Both fossils have enough of the sympod and exopodal scale of a second antenna remaining to justify acceptance of their caridoid nature as illustrated by Peach (1908, pl. 9, fig. 3).

The right counterpart of PY 18821 (Pl. 48, fig. 1) has three joints of a slender, diminutive appendage preserved. Because all eight thoracic appendages are distinguishable as pereopods, they cannot be the remains of a maxilliped. Similar small, slender three-jointed appendages were seen by Peach (1908, pl. 9, fig. 4). They can only represent a mandibular palp. Neither the body of the mandibles nor the maxillae have been seen.

Peach believed the first pair of thoracic appendages had the endopods modified as massive maxillipeds whereas the seven succeeding pairs were constructed alike. All eight pairs are similar on PY 18821 and PY 18884. The five jointed endopods are slender. The three joints beyond the knee together are equal in length to the two proximal joints. The vagueness of the sympods and exopods makes it impossible to correctly portray these structures. Peach encountered the same difficulty. *Crangopsis socialis* Salter close relative of *Anthracophausia Crangopsis socialis* Salter, (Peach, 1908, pl. 10, fig. 11) is restored as having a typical flagellate exopod. *C. rhodesi* Peach (1908, pl. 11, fig. 14) is shown with a marsupium. These structures may have been similarly developed on *Anthracophausia*. The luminous organs and gills reported by Peach (1908, p. 65, p. 69) are unequivocally rejected.

The course of the intestinal tract is clearly impressed on both specimens by detrital fillings of the intestine as is also true of the species from Scotland.

The six somites of the abdomen are covered by subequal tergites. The third, which provides the principal flexure of the abdomen, is the longest and has the greatest depth. The pleural processes are bluntly rounded. I have no basis for addition or subtraction from Peach's (1908, p. 65) description of sexually dimorphic pleopods.

Remnants of the single joint of the sympod and both rami of the uropods and a side view of the telson are preserved on PY 18821 (Pl. 48, fig. 1). For details we must rely upon the restoration presented by Peach (1908, pl. 9, fig. 9) of the caudal fan of *A. dunsiana*. It is reproduced herein (Text Pl. 8, fig. e). The uropods are typically caridoid with furcal lobes and a fixed median plate on

the telson. There can be no doubt that the telson of the Recent Euphausiacea has been derived from such a structure.

Synopsis.—*Anthracophausia* has morphological characteristics suggesting relationships to the Euphausiacea. Particularly significant are the eight pairs of unmodified biramous thoracic appendages, with long slender endopods and the structure of the telson. A noneuphausiid characteristic is the lack of fusion of the carapace with the thoracic somites. It is inferred that a marsupium may have been present as one has been reported on a closely related genus.

The new species is distinguished from *A. dunsiana* Peach by the shape of a stout wedgelike rostrum and the rounded margins of the abdominal pleural lobes.

Stratigraphic occurrence.—Francis Creek shale, Carbondale formation, Alleghany series (Westphalian), Pennsylvanian in the Mazon Creek nodules.

Locality.—Mazon Creek, Grundy County, Illinois.

Collection.—Two specimens are in the Peabody Museum, Yale University. Both were collected by S. S. Strong.

Types.—Holotype is PY 18821 (counterparts a and b) and the paratype is PY 18884. They are in the type collection of the Peabody Museum at Yale University.

Genus **BELOTELSON** Packard, 1886

Because the elements of the caudal fan preserved on fossils of this crustacean are styloid, it was originally assigned with the syncarid genus *Acanthotelson*. The type species is *Acanthotelson magister*.

This caridoid crustacean must have originally had a carapace though it is unknown. The genus is best distinguished by the narrow, spikelike shape of the telson which is unique among Crustacea with large abdomens. The terminal one-quarter of the telson appears to be separated from the main body of the telson by a restriction in width and an articulation. As on the broader telson of *Anthracophausia*, this may be the site of origin of the furcal lobes.

Belotelson magister (Packard), 1886 Pl. 52, figs. 1-4; Text Pl. 9, figs. b, e

Acanthotelson? magister Packard, 1886 a, p. 127, pl. 1, fig. 2, pl. 2, figs. 4, 5.

Belotelson magister, Packard, 1886 a, p. 128.

Belotelson magister, Van Straelen, 1931, p. 13.

This large, prawnlike fossil with a styloid telson and a narrow bladelike exopod of the uropods has no known parallel among Paleozoic Crustacea. Description of the specimens is presented as a specific diagnosis.

Description of the specimens.—Only three specimens of this rare crustacean are available for study; two of these are Packard's types. The specimen upon which Packard described the species was collected by J. C. Carr at Mazon Creek. This is number 38844 (401 a and b) in the collections of the U.S. National Museum. A supplementary note by Packard was appended to his text prior to publication in which a brief description is given of an additional specimen collected by R. D. Lacoë from the subsurface mines near Braidwood in Will County, Illinois. This plesiotype, USNM 38844 (401 c), is better preserved; hence the uniqueness of the species was verified and the generic name, *Belotelson*, proposed. Among the hundreds of Mazon Creek concretions examined in this study, only one additional specimen was discovered. It is number 888 of the Chicago Museum of Natural History.

The specimens are poorly preserved compressions with little relief. Disintegration of the chitin of the exoskeleton has resulted in a reticulate pattern of cracks. As far as known, the original surface texture of the integument was smooth.

The holotype (Pl. 52, fig. 2, 3) presents a dorsal aspect of the abdomen and telson with only fragments of the two pairs of antennae remaining of the anterior position of the body. The plesiotype of Packard (Pl. 52, fig. 1) has its flexed abdomen compressed laterally, but the remains of both pairs of antennae are oriented in the plane of bedding. The new specimen has only the posterior abdominal somites and part of the caudal fan preserved.

Packard recognized two pairs of antennae, but his presentation is confused. The first pair of antennae has a peduncle of three segments; the second and third together are about equal to the length of the stout basal joint. Two flagella from one and the inner flagellum of the other are all that can be detected of the first antennae on the holotype. These are the long antennae mentioned by Packard. The rami are unequal, but a statement as to their true length is not justified.

The basal portions of the second pair of antennae are present. The sympod appears to consist of a single large segment, but there is some indication on the fossils of a second. This joint, if it exists, is not produced as a scape for the antennal scale as is typical in the other Paleozoic Eumalacostraca. The squamate exopod is best seen on the holotype (Pl. 52, fig. 4). The endopod consists of two joints and a flagellum. Compressions of a long stout joint of the left and right appendages are present on both specimens. It is three times longer than the terminal joint from which the flagellum originates. Traces of the flagellum consist of two basal annuli on the left antenna of the plesiotype. Shrinkage cracks have fragmented the integumental remains of the antennal joints. This misled Packard into interpreting them as six annuli of a flagellum.

Little, if any, displacement of parts has occurred in the plesiotype; therefore, the distance between the base of the antennae and the first abdominal segment is a valid measure of the length of the cephalothorax. The combined length of the head and thorax is believed to have been one-third that of the abdomen. The discrepancy between the estimated total length of the two specimens, *i.e.*, 72 mm. and 82 mm., exclusive of the antennae and telson given by Packard, is due to deformation of the holotype when it was a decaying cadaver.

If a carapace originally existed, it left no trace in either specimen.

Remnants of five slender thoracic pereopods are present on the plesiotype. Though only two joints distad of the "knee" can be distinguished, there may have been three. The number of pereopods and their position are suggestive of specialization toward a decapodous adaptation.

The features of the abdomen and telson were given by Packard as the characteristics of the species and genus. The development of the abdomen conveys an impression of a prawnlike decapod. The second and the last somites were the longest. The skeletal remains in the holotype have been spread laterally exaggerating its true width. The laterally compressed abdomen of the plesiotype presents the tergite and pleural lobes in their true perspective. The first abdominal segment is smaller than the second. The abdomen then

tapers to the sixth segment. All except the last abdominal segment bear pleural lobes. Developed mid-dorsally on the sixth abdominal tergite is a carinate ridge.

Details of the abdominal appendages are not known except for the uropods, though obscure relics of pleopods are present on the second abdominal somite of the plesiotype. Superficially the uropods resemble those of *Acanthotelson*. From a stout basal joint, a bladelike ramus arises. Whereas the exopods are straight and spike-like in *Acanthotelson*, they are narrow blades in *Belotelson*. The outer edge of the exopod is nearly straight except the extremity which bends slightly outward. The inner margin is much less strongly chitinized and is curved throughout most of its length. The endopods are not known. The scapulate remains of the rami of the uropods are present on all three specimens. These sclerotized structures may not be representative of the complete exopods. It is common for only the outer edge of the lobes of the uropods to be strongly fortified as in Recent species of *Panulirus* and the Paleozoic species of *Anthracophausia*. Thus the inner more membranous lobes of the exopods may have been destroyed as were the endopods.

From a broad base the telson narrows rapidly and then extends as a spine. At a position about three-quarters of its length it narrows. The tip of the spinelike telson is an articulated process. The abrupt narrowing at the articulation may indicate the position of origin of a caudal furca.

Synopsis.—Morphological information is too meager for adequate definition of *B. magister*; nevertheless, the details of its morphology clarified above prove that it is not a syncarid. Absence of a carapace on the three poor fossils that have been collected is negative evidence. It does not prove that such a structure was not present in life. In fact, lack of preservation of the cephalothorax may be an argument for a protective dorsal shield. Inadequate fossilization of this part of the body is common among caridoid fossil Crustacea. The decapodous adaptive trend of the thoracic pereopods and the large size of the abdomen relative to the estimated length of the cephalothorax are the only criteria on which we can rely. Until proven otherwise, *Belotelson magister* Packard must be classified with the Paleozoic Malacostraca with a carapace.

The abdominal tergites, particularly that of the sixth abdominal somite, and the scapulate outer sclerotized portions of the rami of the uropods in *Palaeomysis* (Peach, 1908, pl. 8, figs. 13, 14) and *Anthracophausia* (Peach, pl. 9, figs. 9, 11) superficially resemble those of *Belotelson*; however, the greater width of the telson distinguishes these genera.

Stratigraphic occurrence.— Francis Creek shale, Carbondale formation, Alleghany series (Westphalian), Pennsylvanian in Mazon Creek nodules.

Localities.— Grundy and Will counties, Illinois.

Types.— Holotype and plesiotype, USNM 38844.

Genus **ARCHAEOCARIS** Meek, 1872

The carapace, six abdominal tergites, telson, and a three jointed "leg-like appendage" were mentioned by Meek (1872) in the original description of the fossils for which the generic name, *Archaeocaris*, was provisionally established. A relationship with the Recent cumaceans was suggested for these Lower Mississippian Crustacea (1872, 1875). Ortmann (1897) superficially examined several excellent specimens and noted four free thoracic tergites underlying the carapace. This led him to believe *Archaeocaris* was a synonym of *Crangopsis* and an affinity with the Mysidacea was postulated. If either Meek or Ortmann had closely examined the specimens before them, they would have discovered features of the Stomatopoda. The following description is based on the holotype and paratypes of Meek and the plesiotypes of Ortmann. No additional specimens of this species are known to have been collected.

The cephalothorax of *Archaeocaris* is one-third the body length. The carapace is without ornament. There is no mid-dorsal carina or transverse sulcus. Articulated to the carapace is a platelike rostrum. The endopods of some of the thoracic appendages are clustered forward under the cephalothorax. These subchelate appendages are believed to be pairs two to five. The six somites of the abdomen are large and their pleurae are truncated. Rami of the caudal fan are broad blades and the telson is spatulate.

Perimecturus (Peach, 1908, p. 39-53) and *Archaeocaris* have several characteristics in common. For purposes of comparison, I

have taken the liberty of preparing a restoration of *P. elegans* Peach (Text Pl. 8, fig. c). It is a composite of the characters illustrated in Peach's (1908, pl. 6, figs. 2-6) work. Features of special note on *Perimecturus* are the articulated rostrum, four free thoracic somites, shallowness of the small carapace, large abdomen, and the biramous nature of the three posterior thoracic legs. Peach figured flagellate exopods but mistook remains of the jointed endopods for a brood pouch (1908, pl. 6, fig. 2), and the broad lobes shown on *P. pattoni* as a "broodpouch" are probably the remains of pleopods (1908, pl. 6, fig. 9). The differences in the structure of the anterior thoracic appendages from those of *Archaeocaris* (Text Pl. 8, fig. a) are believed to be due to incompleteness or misinterpretation of the Scottish fossils.

Whereas *Perimecturus* has narrow, hastate, uropod rami, the species of *Archaeocaris* have broad caridoid lobes. The genera differ also in that *Perimecturus* has carinae on the carapace and the abdominal tergites and spines are present on the outer margin of the exopod of the uropods.

In addition to the type species, *A. vermiformis* Meek, a new species is herein described from the Upper Mississippian of Oklahoma. *Perimecturus fraiponti* Van Straelen (1922) from the Westphalian of Belgium should be assigned also to *Archaeocaris*; thus, the known stratigraphic range of the genus is Lower Mississippian to Middle Pennsylvanian.

Archaeocaris vermiformis Meek, 1872 Pl. 45, figs. 1-4; Pl. 46, figs. 1-3;
Pl. 53, fig. 5; Text Pl. 8, fig. a

Archaeocaris vermiformis Meek, 1872, p. 335-336.

Archaeocaris vermiformis, Meek, 1875, p. 321-322, pl. 18, fig. 7.

Crangopsis vermiformis, Ortmann, 1897, p. 283-289.

Archaeocaris vermiformis, Van Straelen, 1931, p. 71.

A. fraiponti (Van Straelen) and the new species from Oklahoma are too poorly known for adequate specific characterization at this time. If it were not for the uniform small size of *A. vermiformis* and massiveness of its mandible, it would be impossible to distinguish it from the new species to be described from Oklahoma.

Description of the specimens.—The specimens are preserved in gray phosphatic concretions. Not only is there a concentric structure

of the phosphatic material around the fossils, but with few exceptions, the skeletal remains have not been compressed. The interior spaces of the skeletons are filled with radiating calcite crystals with small amounts of pyrite and glauconite; therefore, the concretions are believed to be syngenetic. Original exoskeletal material is preserved with degradation of only the organic base. It is now a brittle, gray to brown, translucent substance. Evidently, the exoskeleton was impregnated by calcareous material in life.

Twenty-five specimens, some with counterparts, have been studied. Measurement of body length could be made on 13 of these. The range was from 16 mm. to 25 mm. One-half the specimens measured were between 24 and 25 mm. long, rostrum and telson not included. On no specimen that the body length could be determined, is the carapace complete. For the six specimens on which the length of the carapace could be estimated with reasonable accuracy, it was one-third the body length. The holotype (USNM 27126, Pl. 46, fig. 1) has a body length of 22 mm., carapace length of 7.5 mm. (estimated) and the length of the second abdominal tergite is 2.4 mm. A plesiotype (PU 1597 ^a/4) with a body length of 25 mm. has a rostrum 1.1 mm. long, carapace 8 mm. long (estimated) and telson 5 mm. long.

The carapace covers the head and thorax, but in all specimens its posterior is broken. Its features are best seen on PU 1597 ^a/3 (Pl. 45, fig. 1) and PU 1597 ^a/1 (Pl. 46, fig. 2). The carapace has its greatest depth posterior and it becomes very shallow anteriorly. There is no antero-lateral angle; rather, there is a curvature and rapid narrowing of the carapace immediately behind the rostrum. The free margins are bordered by a narrow rim. A triangular rostral plate articulates with the carapace (PU 1597 ^a/3, Pl. 45, fig. 2). Its length is equal to its basal width. The anterior apex is rounded. Carinae are absent from the rostrum as well as from the carapace.

The carapace seems to have been fused with four thoracic somites. On no specimen can more than four free tergites be seen (PU 1597 ^a/2, Pl. 46, fig. 3). The tergite of the eighth thoracic somite is twice the length of the fifth.

Of the cephalic appendages, only the right mandible was seen on PU 1597 ^a/5 (Pl. 45, fig. 4). From the condyle, it widens into

the stout body of the mandible. The anterior is nearly straight whereas two bulges of the posterior are separated by a transverse sulcus. There is a strong posteriorly directed gnathic process. The palp and molar process were not seen. Among Recent Crustacea, it is only in the Stomatopoda that one finds the mandible comparably developed (Text Pl. 8, fig. d).

The remains of the thoracic appendages are clustered together making it difficult to interpret their structure; nevertheless, four pairs of subchelate appendages can be distinguished, each with six joints. The proximal joint is short and dorso-ventrally oriented (PU 1597 ^a/5, Pl. 53, fig. 5). This is probably equivalent to the complete sympod. An elongate forward projecting joint, probably the ischium, articulated with this. Those of three legs can be seen on PU 1597 ^a/2 (Pl. 46, fig. 3). The next leg joint is short and projects inwardly (PU 1597 ^a/3, Pl. 45, fig. 1). The knee is at the distal articulation of this element, the merus, beyond which there are three joints. Two stout broad joints (PU 1597 ^a/3, Pl. 45, fig. 1; PU 1597 ^a/1, Pl. 46, fig. 2; and PU 1597 ^a/2, Pl. 46, fig. 3) are oriented ventro-posteriorly. The mesad margin of the most distal of the two, the propodus, is armed with a row of small conical spines (PU 1597 ^a/1, Pl. 46, fig. 2) much as on the "palm" of *Chloridella*. A dactylus opposes the propodus to form a subchela. It can be seen on PU 1597 ^a/1 (Pl. 46, fig. 2) and PU 1597 ^a/5 (Pl. 45, fig. 4). It is believed that these four pairs of raptorial legs are the second to fifth appendages. This interpretation is based on their position and by analogy with the Recent stomatopods. The new species from Oklahoma has traces of additional thoracic legs that may have been pereopods.

Peach (1908, p. 38-46) claimed the thoracic appendages of *Perimecturus* were biramous and bore oostegites on females. The three basal joints of the four pairs of clustered appendages portrayed (1908, pl. 6, fig. 2 a) are identical in structure to those seen on *Archaeocaris*. It is believed the spatulate joint shown by Peach is a fragment of the carpus and is not the terminus of the leg. Restudy of the specimen of *Perimecturus* is required before conclusive interpretation of the legs of this genus is possible.

The abdomen is enormous relative to the size of the cephalothorax (USNM 27126, Pl. 46, fig. 1). It is believed the first ab-

dominal somite was somewhat larger than the other five which are subequal in length. The abdomen narrows and decreases in depth posteriorly. The pleurae of each tergite are broad lobes which have their ventral margin truncate. The ventral edge originates through an anterior curvature of small radius.

Only the appendages of the sixth abdominal somite, the uropods, are known (PU 1597 ^a/₄, Pl. 45, fig. 3). The sympod of the uropod is long and narrow and it is believed the two rami were lobate. The remains are too incomplete to determine if the exopod consisted of two joints, a characteristic feature of the Recent stomatopods.

The telson is spatulate. Its basal portion is highly arched and there is a mid-dorsal carina. There is suggestive, but inconclusive, evidence of furcal lobes and a median articulated spine.

Synopsis.—Most of the morphological characteristics of *Archaeocaris vermiformis* that can be determined are those of the Stomatopoda. They are the relatively large size of the abdomen, small carapace not fused with last four thoracic tergites, articulated rostrum, shape of mandible, and the presence of four pairs of subchelate thoracic appendages. In common with the caridoid Paleozoic fossils, it has a single joint in the sympod of the thoracic legs and furca and a median spine on the telson. It is believed that *Archaeocaris* and *Perimecturus* are closely related.

Stratigraphic occurrence.—New Providence fm., Kinderhookian, Lower Mississippian.

Locality.—Linietta Springs, Junction City, Boyle Co., Kentucky.

Collections.—Holotype and seven paratypes (13 pieces) are catalogued as 27126 in the collection of the U.S. National Museum. Twenty-seven pieces representing 18 individuals are in the collections of Princeton University, 1597 d. The specimens herein figured have been assigned suffixes.

***Archaeocaris graffhami*, new species** Pl. 47, figs. 1-4; Text Pl. 8, fig. b

A single specimen of a large species of *Archaeocaris* was discovered in the Caney shale of Upper Mississippian age in Oklahoma. Size alone is a poor basis for distinguishing species of fossils and except for the relatively small size of the mandible, all characters that

can be determined are identical to those of *A. vermiformis*. In the new species the mandible is much less massive, *i.e.*, *A. vermiformis* $\frac{(\text{mandible width}) 0.9 \text{ mm.}}{(\text{body length}) 21 \text{ mm.}} = .043$, whereas on Oklahoma specimen $\frac{0.8 \text{ mm.}}{35 \text{ mm.}} = .023$. Until better specimens of *A. graffhami* are collect-

ed, the species is characterized by the weaker development of the mandible. A diagrammatic drawing of the fossil, with parts labeled, is presented in Text Pl. 8, fig. b. The species is named in honor of its collector, Allen Graffham.

Description of the specimens.—Though the exoskeleton is fortified with calcareous materials, it is badly crushed. The fossil is nearly flat. Within the tan argillaceous limestone matrix, the fossil lies obliquely oriented in a more or less dorso-lateral position. This slanted position in connection with compressional spreading has greatly exaggerated the apparent depth of the animal.

Neither extremity of the fossil has been retained; however, the distance from the anterior of the carapace to the base of the telson is estimated to be 35 mm. The following lengths were also determined: head and thorax, 12.0 mm.; seventh thoracic somite, 1.0 mm.; eighth thoracic somite, 2.0 mm.; abdomen 23.0 mm.; first abdominal somites, 3.6 mm. each.

The carapace is broken away beyond the fourth thoracic somite leaving four tergites uncovered. The small shallow shield is unornamented. A cervical groove, carina and sulcus were not seen. Its anterior and lateral margins are too poorly preserved for accurate delimitation. The rostrum is unknown.

Only the body of a mandible with the peculiar transverse sulcus of the type species can be seen of the cephalic appendages.

The four exposed thoracic somites gradually increase in size posteriorly. The tergite of the eighth thoracic somite is more than twice the width of the fifth.

A congeries of small thoracic appendages is clustered forward under the carapace. No interpretation of structure of these appendages is possible. That the appendages of the last somites are different is proven by remains of legs of larger size which apparently extended ventrally. A short proximal and a long distal joint of the

eighth and a single joint of the seventh are exposed (Pl. 47, fig. 1).

The abdomen constitutes two-thirds of the animal's length. A portion of its great depth is due to compressional expansion of the tergites, but there can be no doubt that it was enormously developed. The first abdominal tergite is about one-half again as long as the five subequal tergites succeeding it. The tergites are smooth. The truncated free ventral edges are rectilinear except for an anterior curvature. They are reinforced by a narrow rim.

It is unfortunate that the important taxonomic characteristics of the element of the caudal fan are not more clearly visible. The uropods and telson have been crushed together. The uropods have a relatively long sympod. The blade of the exopodal joint is broad (Pl. 47, fig. 3). The telson was wide at the base and evidently was longer than the uropods. Nothing more is known.

Stratigraphic occurrence.—Delaware Creek member, Caney shale, Chesterian, Mississippian.

Locality.—N.W. 1/4, Section 27, T. 3 N., R. 6 E., Pontotoc County, Oklahoma.

Collector.—Allen Graffham of Ardmore, Oklahoma.

5879 *Types.*—The holotype is number 5849⁶ in the Museum of Comparative Zoology at Harvard University. The less complete counterpart is number 4411 in the Paleontology Collection of the University of Oklahoma.

Genus **ACADIOCARIS**, new genus

Palaecaris novascotica Copeland (1957 a, p. 596) from the Mississippian deposits of Nova Scotia has many characteristics in common with a Pennsylvanian species from Scotland, *P. landsboroughi* Peach (1908, p. 55, 56). Both have only 12 free post-cephalic somites exposed. Calman (1932 b) recognized the phylogenetic significance of another Scottish species, *P. scotia* Peach, which also has the first two thoracic somites obscured by a short carapace, and he established a new genus, *Anthracocaris*. The Canadian species is the first American representative of these Paleozoic tanaidacean-like Crustacea, but it cannot be assigned to Calman's genus, as Rolfe (1962, p. 549) suggested. It is conspicuously distinguished by the elements of the caudal fan.

Though I have not seen the specimens described by Copeland, it is apparent from the photographs presented (1957 a, pl. 67, fig. 4; pl. 68, figs. 1-9) that his morphological characterizations are incorrect, *e.g.*, (p. 596-597) "Thoracic segments . . . each with . . . a pair of long uniramous limbs, limbs equal to one-third the length of the body, each three-jointed, proximal segment the longest, non-chelate" and "Abdominal segments . . . having a pair of short, three-jointed uniramous limbs; last abdominal segments slightly longer than wide, with no limbs, bearing the telson and uropods." Not only do the photographs disprove his proportions and interpretation of jointing of the legs, but the uropods are the "limbs" of the sixth abdominal somite!

Acadiocaris has only 12 postcephalic somites evident on the fossils illustrated. This means that the first two thoracic somites are either fused with the head or they are covered by a short carapace as in *Anthracocaris*. The new genus differs by having a spatulate telson very much like that of *Palaeocaris*. The uropods are distinguished by being relatively narrow blades. The endopods of the thoracic appendages are shorter and stouter than those of *Palaeocaris*. In this respect they are comparable to those of *Palaeosyncaris*.

The type species is *Palaeocaris novascotica* Copeland.

***Acadiocaris novascotica* (Copeland), 1957**

Palaeocaris novascoticus Copeland, 1957 a, p. 596-597, pl. 67, fig. 4; pl. 68, figs. 1-9.

Palaeocaris novascotica, Rolfe, 1962, p. 549.

Morphological interpretations herein presented are based upon the photographs published by Copeland. When the fossils preserved as carbonized compressions are restudied, a more detailed description will be possible.

The carapace and six exposed thoracic somites are equal to four-sevenths the length of the body (1957 a, pl. 68, figs. 6, 9). The carapace, including the head shield, is equal to one-sixth the body length. Copeland presented no measurements. If the indicated enlargements of the photographs are correct, the holotype, GSC 13316, is 10 mm. long, telson not included. The length of GSC 13323 is 7 mm. and GSC 13320 is 8 mm.

Morphology.—A small carapace covers the head and the two anterior thoracic somites. It is best displayed (Copeland, 1957 a, pl. 68, fig. 6) on GSC 13320. A small portion of the second thoracic somite extends from under the carapace on this specimen. Other details of the carapace cannot be determined.

The first antennae are excellent on three of the specimens figured. The three joints of the peduncle are stout. They are distinguished by being subequal in length with the second being the shortest. The internal flagellum is about one-half the length of the outer ramus. Copeland made the contradictory statement "second pair of antennae uniramous, protopodite with three podomeres, bearing a setate rectangular basal scale and a slender flagellum equal to half the length of the body." If a scale is present, the appendage is not uniramous. The scale cannot be seen on the photographs, but he appears to be correct in his observation that the endopod consists of three joints and a long flagellum.

Remains of five of the thoracic appendages are beautifully preserved on the left side of the holotype, GSC 13316, (Copeland, 1957 a, pl. 68, figs. 1, 2). The endopods are short and stout and are less than one-fourth the length of the body. Even in the small photographs published (X 4), the dactylus, propodus, carpus and merus are clearly evident on the posterior leg. The long merus above the knee is best seen on the two preceding legs. The shape of these joints is typical. There is no reason to believe that the basal joint of the endopod, the ischium, and the joints of the sympod are not present. No proof is presented by Copeland that the thoracic legs are "uniramous". Close scrutiny of the specimen will probably reveal vestiges of the ischium, sympod, and the exopod.

The abdominal somites decrease in size, but are subequal in length except the sixth abdominal somite which is twice as long as the others. The tergites of body somites 14 to 18 have their pleurae anteriorly rounded with a blunt point at their post-lateral angle (GSC 13323, Copeland, 1957 a, pl. 68, fig. 9). Relics of the pleopods shown on the same photograph do not corroborate the statement that these appendages were "three-jointed uniramous limbs".

The uropods as shown on GSC 13321 (Copeland, 1957 a, pl.

68, fig. 7) characterize this genus. The sympod is small. The exopod is long and bladelike. The slight convexity of its outer margin terminates at a position equal to two-thirds the length of the ramus where a transverse suture on the blade separates a narrowing terminal lobe. The length and width of the endopod are the same as those of the exopod.

The telson is spatulate (Copeland, 1957 a, pl. 68, fig. 7) with its greatest width near the base. No articulated furcal structures are associated. At least the terminal edge of the telson bore stout bristles. There are suggestions on the photograph that the lateral margins were also armed.

Synopsis.—This crustacean, previously referred to *Palaeocaris*, has a carapace covering the first two thoracic somites. It differs from *Anthracocaris scotica* in the narrow lobate shape of the rami of the uropods. According to Peach (1908, pl. 8, figs. 1, 5) the telson of this species has accessory structures.

The likeness of *P. landsboroughi* Peach (pl. 8, fig. 8-10) to the Canadian fossil must be acknowledged. The uropods are remarkably similar. If *P. landsboroughi* does not have furcal lobes on the telson, the species are congeneric. *Acadiocaris novascotica* is minute and lacks dorsal crests on the thoracic and abdominal tergites.

Stratigraphic occurrence.—Horton group (Upper), Osagean, Lower Mississippian.

Locality.—Core from drill hole one mile south of Hillsboro, Inverness County, N.S., Canada.

Collector.—W. A. Bell.

Types.—Holotype is No. 13316, and paratypes are Nos. 13317-13324 in the collection of the Geological Survey of Canada.

Genus **PALAEOPALAEON** Whitfield, 1880

The materials available to Whitfield (1880) at the time this genus was established are much poorer than one would suspect from the description or the figure (1891, pl. 12, fig. 20). The "specimen" he presented as a carapace, six abdominal tergites and caudal fan, are natural molds of scraps of three separate individuals. The pereopods and pleopods mentioned are not present on any of the syntypes.

There is a note with the syntypes at Columbia University that James Hall of the New York State Museum made impressions for a study that was published later (Hall and Clarke, 1888, p. 203). This "plastotype" is a composite of the syntypes with missing parts crudely restored. Because of the inaccurate interpretation of *Palaeopalaemon*, it has frequently been referred to in the literature as an Upper Devonian decapod.

Though there are differences in ornament between the syntypes and the two additional specimens now available from the Chagrin shale (= Erie shale of Whitfield) east of Cleveland, there is no reason to believe that two species are represented. The two syntypes displaying the ornament pattern on the carapace have a pattern of anastomosing fine ridges whereas one of the additional specimens recently collected has a pattern of minute papillae. Another has a subdued ornament that is intermediate. For morphological interpretation, a specimen from the Lower Mississippian of Kentucky has proven most useful. The latter specimen has the characteristic anastomosing pattern of the syntypes on its carapace. The restoration presented in Text Pl. 9, fig. a, shows only the features distinguished on these specimens. Specimens of an additional species, *P. iowensis* Walter from the Lower Mississippian of Iowa, have been of little use in the interpretation of the morphology of this genus.

Palaeopalaemon was shrimplike; however, the cephalothorax is only slightly shorter than the abdomen. None of the thoracic tergites is believed to have been normally exposed at the broad dorsal posterior re-entrant of the carapace. The carapace has its greatest depth just anterior to the postero-lateral curvature. Its depth decreases gradually anteriorly where the carapace becomes unusually shallow. The most distinctive characteristics of this genus are the mid-dorsal and lateral pair of longitudinal carinae, narrow anterior doublure, bifurcating cephalic sulcus and an oblique shoulder on the dorsum of the carapace. Anterior to the cephalic sulcus, the lateral carinae become prominent crests and terminate as spines. A rostrum was probably present. The peduncles of the first pair of antennae are abnormally large. It is believed the thoracic appendages were biramous, but only the long slender endopods have been observed.

They are all pereopods. The last somite is longer than the five preceding abdominal somites, the tergites of which have rounded pleural lobes. Of the abdominal appendages, only the uropods are known. They have a short single-jointed sympod. The single exopod that has been studied is subtriangular with the greatest width distad.

The type species is *Palaeopalaemon newberryi* Whitfield from the Upper Devonian and Lower Mississippian.

Palaeopalaemon newberryi Whitfield, 1880 Pl. 49, figs. 1-3; Pl. 50, figs. 1-8; Pl. 51, fig. 5; Text Pl. 9, fig. a

Palaeopalaemon newberryi Whitfield, 1880, p. 41-42, (fig. in author's separates).

Palaeopalaemon newberryi, Hall and Clarke, 1888, p. 203-205, pl. 30, figs. 20-23.

Palaeopalaemon newberryi, Whitfield, 1891, p. 571, pl. 12, figs. 19-21.

Palaeopalaemon newberryi, Whitfield, 1893, p. 461, pl. 8, figs. 19-21.

Palaeopalaemon newberryi, Beurlen, 1930, p. 443, fig. 63.

Palaeopalaemon newberryi, Van Straelen, 1931, p. 30.

The only criterion justifying recognition of two species of *Palaeopalaemon* is the ornament on the carapace. On *P. newberryi* there is an anastomosing network of ridges or small papillae whereas on *P. iownesis* the carapace is smooth but punctate. No significant morphological differences have been determined and those presented by Walter (1917, p. 122, 123) are erroneous. Of the two species, *P. newberryi* is somewhat smaller.

Description of the specimens.—The specimens from Ohio are preserved in dark gray, argillaceous, siderite concretions from the black Chagrin shale. None of the specimens displays any compressional distortion. The more complete specimen from the Lower Mississippian of Kentucky is preserved in a gray phosphatic concretion. It is deformed despite the fact that these concretions are believed to be syngenetic. The remains of the exoskeletons from both deposits appear to have originally been impregnated with mineral matter.

The only specimen with the elements of the cephalothorax and abdomen articulated is MCZ 5880 (Pl. 49, fig. 3; Pl. 51, fig. 5). On this specimen the carapace is 22 mm. long and the body length, telson not included, is estimated to be 50 mm. One of the syntypes is a natural mold of an incomplete carapace. From this (CU 5514), it is estimated that the carapace was 21 mm. long. Two other speci-

mens without the abdomen preserved have been found. Their carapace lengths are 19 mm. and 18 mm.

The restored carapace figured in drawings by Hall and Clarke (1888, pl. 30, fig. 20) and Whitfield (1891, pl. 12, fig. 20) closely resembles the cast (Pl. 50, fig. 8) made from the natural mold believed to be a syntype (CU 5541, Pl. 50, fig. 4). Because both extremities of this specimen are incomplete and the longitudinal carinae have been exaggerated by deformation, the description that follows will be based upon CIMNH 7628 (Pl. 50, figs. 5, 7) and MCZ 6563 (Pl. 50, fig. 1). The lateral flaps of the carapace have their greatest depth posteriorly. Broadly rounded lobes extend posteriorly below the re-entrant of the postero-dorsal margin. A narrow thickened rim borders the posterior edge of the carapace. A keel that originates at the postero-lateral curvature of the carapace develops into a flexure anteriorly such that the free ventral anterior margin is bent under to form a narrow doublure. There are three longitudinal carinae, a mid-dorsal and a dorso-lateral pair. They are interrupted in the vicinity of the cephalic sulcus. There is no trace of the mid-dorsal ridge for a short distance; it then increases greatly in height and massiveness anteriorly as if it were to give rise to a rostrum. However, a rostrum has not been observed. The lateral pair of carinae are interrupted for a short distance by the transverse cephalic sulcus; they increase in amplitude near the anterior of the carapace and it is believed they terminated in gastric spines. The anterior portion of all carapaces examined were too poorly preserved for positive interpretation. A prominent shoulder projects obliquely backwards across the dorsum of the hepatic portion of the carapace from the interruption of the lateral carina by the cephalic sulcus. From its origin at the ventral flexure to the position of the lateral carina, the cephalic sulcus is a simple groove. Above this, it divides into two prongs; one bends anteriorly and the other associated with the shoulder extends obliquely backward. Near its postero-dorsal termination the posterior branch diverges dorsally away from the shoulder. It terminates without intersecting the mid-dorsal carina. This branch of the cephalic sulcus is the cervical groove.

The ornament on the carapace of *Palaeopalaemon* is a specific criterion. On the two pieces of the carapace represented by the syn-

types (CU 5514, Pl. 50, fig. 4 and CU 6174, Pl. 50, fig. 2) there is a system of anastomosing fine ridges oriented in an antero-ventral to postero-dorsal direction. This pattern is also present on the specimens from the Lower Mississippian (MCZ 5880, Pl. 49, figs. 1-3; Pl. 51, fig. 5). Two additional specimens from the same stratigraphic horizon as the syntypes, the Chagrin shale, display a variation from this pattern. On C1MNH 7628 (Pl. 50, fig. 7) the ornament is a fine papillae whereas a subdued intermediate ornament is present on MCZ 6563 (Pl. 50, fig. 1).

The remains of both pairs of antennae that have been seen are only peculiar in the gigantic size of the peduncle of the first antennae. Only one enormous segment of this appendage has been observed (C1MNH 7628, Pl. 50, fig. 7; CU 5514, Pl. 50, fig. 8, and MCZ 5880, Pl. 51, fig. 5). It must be the basal joint of the three-jointed peduncle. Remains of the two flagella were not seen. Fragments of the sympod, scale and endopods, both joints and annuli, of the second antennae are present on MCZ 5880 (Pl. 51, fig. 5). The scale is better seen on a specimen of *P. iowensis*, MCZ 5106 (Pl. 51, fig. 1). The small jointed structure above the scale but associated with it is not the base of a first antenna as interpreted by Walter (1917, p. 121, pl. 5 a, fig. 1). It is the basal jointed section of the endopod of a second antenna.

Though reported by Walter (1917, p. 121), authentic eyes have not been observed on either species of this genus.

A badly preserved mandible is present on MCZ 5880 (Pl. 49, figs. 2, 3). There is a long mandibular body with a single apical condyle. As far as can be seen, the incisor and molar processes are typical. No remains of the palp are present. Posterior and ventral to the mandible is a congeries of small appendage parts. Some are the remains of jointed rami whereas others are foliaceous. These are, no doubt, the remains of the two pairs of maxillae.

It is presumed the carapace was not fused with the thoracic somites. The only evidence presented by the fossils bearing on this is the disarticulated and displaced nature of the sternites. The scraps of the sternites (MCZ 5880, Pl. 49, figs. 1-3) suggest broad transverse sclerites as on the pygocephalomorphs.

There are remains of five anterior thoracic endopods with

minute scraps of two additional legs on the right side on MCZ 5880 (Pl. 49, fig. 3). From their position it is believed the sixth pair of legs are the appendages not represented. All of the legs were developed as long slender pereopods. There is no reason to believe that any of them were modified for raptorial purposes. Walter (1917, p. 122) mistakenly interpreted the large joints of the peduncle of the first antennae as the bases of an enormous pair of thoracic legs. Evidence of exopods and oostegites are lacking. This is probably due to a deficiency of the fossils.

Six abdominal somites can be distinguished on MCZ 5880 (Pl. 51, fig. 5). The first five tergites are subequal and the last is about half again longer (CU 6714, Pl. 50, fig. 6). They bear the same ornament as the carapace. The pleurae are distinguished from those of other Paleozoic Crustacea by being broadly rounded (CU 6174, Pl. 50, fig. 2, and MCZ 5880, Pl. 51, fig. 5).

The only abdominal appendages seen were the uropods and these are on one of the isolated fragments constituting the syntypes (CU 6714, Pl. 50, figs. 3, 6). The figure and description presented by Whitfield (1891, p. 461, pl. 8, figs. 20, 21) of the caudal fan are wrong. There is a short stout sympod. Only one of the two rami is preserved, and it is a subtriangular lobe with the greatest width near its extremity. Its distal edge is broadly rounded. A branching ridged ornament is evident on this, the exopod. Nothing of the telson is known.

Synopsis.—*Palaeopalaemon newberryi* has morphological characteristics consistent with those of other caridoid Paleozoic Eumalacostraca. The carapace is distinguished by the branching of the cephalic sulcus, dorsal oblique shoulder posterior to the cervical groove, a dorsal and a pair of lateral carina, and a small doublure on the carapace. In common with *Eocaris* (Brooks, 1962 a) (Text Pl. 9, fig. e) the peduncle of the first antenna is abnormally large; however, the pleurae of the abdominal tergites are rounded and the exopod of the uropod is a broad subtriangular lobe. The ornament is a specific criterion.

Stratigraphic occurrence.—Chagrin shale member, Ohio shale (= Erie shale), Upper Devonian, and the New Providence fm., Kinderhookian, Lower Mississippian.

Collecting localities.—The syntypes are from near Leroy, Lake County, Ohio; CIMNH 7628 was collected in Stebbins Gulch, Lake County, Ohio; MCZ 6563 was collected near Painesville, Lake County, Ohio, and MCZ 5880 was collected at Blue Mound west of Junction City, Boyle County, Kentucky.

Types.—Three fragmentary syntypes and a vial of 18 small rock fragments are in the collection of Columbia University. They are catalogued as 5514, 6174, and 6714. Artificial “plastotypes” are present in the collection of the New York State Museum (4607) and the U.S. National Museum.

Palaeopalaemon iowensis Walter, 1917

Pl. 51, figs. 1-4

Palaeopalaemon newberryi, Whitfield, 1892, p. 237-238.

Palaeopalaemon newberryi, Weller, 1900, p. 69.

Palaeopalaemon iowensis, Walter, 1917, p. 119-123, pl. 5 a, figs. 1-4.

Palaeopalaemon iowensis, Van Straelen, 1931, p. 30.

This species is distinguished by having a smooth exoskeleton with small pits rather than an ornament in relief, and the individuals are larger. Morphologically the two species assigned to this genus are identical.

Description of the specimens.—Only three specimens have been closely examined. There is one fragmentary species with the carapace, portions of the second antennae and a pereopod preserved in the Museum of Comparative Zoology. Two other specimens with portions of the carapace preserved are in the collections of the U.S. National Museum. The holotype and several fair specimens in the collections of Iowa State University have been subjected to only cursory examination. When these specimens are made available to me for proper study it is believed that many important morphological features of this genus will be clarified.

The species are preserved in silty, gray, carbonate concretions. The remains have been protected from compressional forces by the syngenetic concretions. The skeletal material is now light grayish-brown and has a bright natural polish. Two of the carapaces are estimated to have had a carapace length of 26 mm. On another it is 31 mm. long. The carapace of the specimen figured as the holotype by Walter is 36 mm. in length.

Morphological characteristics of the carapace that can be determined are exactly as described for *P. newberryi*. That the lateral carinae are developed as gastric spines forward of the cephalic sulcus is proven by USNM 141319. The surface is smooth and polished and all specimens display a fine punctation.

One specimen has the antennal scale partially preserved (MCZ 5106, Pl. 51, figs. 1, 2). Its outer margin is reinforced and is slightly concavely curved. The blade of the scale is a broad lobe. The joints above the scale are the basal portion of the endopod of the same appendage and are not remains of a first antenna as Walter interpreted similar structures on the holotype.

Only one fragment of a leg is present on the specimens studied. The joint is long, slender and round (MCZ 5106, Pl. 51, fig. 4). The pits on it must have been the sites of origin of setae.

Synopsis.—*Palaeopalaemon iowensis* is characterized by its large size and the punctation of the smooth exoskeleton. Morphologically it is identical to *P. newberryi*. None of the morphological distinctions presented by Walter are valid.

Stratigraphic occurrence.—Kinderhook shale, Kinderhookian, Lower Mississippian.

Collecting locality.—All specimens are from Kaskade Creek at the southwestern edge of Burlington, Iowa.

Collections.—The original specimen of Whitfield has not been located. The holotype and several additional specimens are in the collections of Iowa State University. The specimens described above are in the collections of the U.S. National Museum (141319) and the Museum of Comparative Zoology (5106).

Genus **DEVONOCARIS**, Brooks, 1962

A single poorly preserved specimen from the Middle Devonian deposits of New York is of special interest in that it is one of the two most ancient eumalacostracan fossils known. The specimen was originally described as *Palaeocaris? cuylerensis* Wells. Not only is the species not congeneric with *Palaeocaris*, but it has none of the attributes of a syncarid.

The telson of *Devonocaris* has no known parallel. It is spade-

shaped. Though it is nearly rectangular, its margins are slightly convex. Its posterior extremity is as wide as its base. A broad median ridge arises from the arched basal portion and extends the remaining length of the blade. The basal two-thirds of each lateral margin is reinforced by a rib.

All known morphological features are shown on the drawing (Text Pl. 9, fig. d). They will be discussed below in the description of the type species, *Palaeocaris? cuylerensis* Wells (1957). *Palaeocaris destinezi* Van Straelen (1943) is believed to be congeneric.

Devonocaris cuylerensis (Wells), 1957

Pl. 53, figs. 2, 4;
Text Pl. 9, fig. d

Palaeocaris? cuylerensis Wells, 1957, p. 983, 984; pl. 125, figs. 1-4.

Devonocaris cuylerensis, Brooks, 1962 a, in press.

The description of the fossil with measurements was presented by Wells as the specific criteria for distinguishing this species. Morphological reinterpretation requires that new parameters be established. Measurements are as follow: length of body to the base of the telson, 16.8 mm.; cephalothorax, 7.8 mm.; abdomen, 9.0 mm.; telson, 2.7 mm.; length of sixth thoracic somites, 0.6 mm.; length of abdominal somites one to six, 1.5 mm.; and the maximum width of the telson is 1 mm. The fossil appears to have been subjected to very little, if any, lateral spreading, thus it is worthy of note that the first abdominal somite is 2.5 mm. and the last is 1.6 mm. wide.

Description of the specimen.—The holotype, Cornell University 40020, is preserved as a dorso-ventral compression of low relief in a black shale matrix. A carbonaceous residue of part of the chitinous exoskeleton remains. Some fine-grained pyritization has occurred. No other fossils are known.

Remains of the cephalothorax are fragmentary. Except for relics of the narrow tergites of the posterior thoracic somites, the dorsal elements of the exoskeleton were broken away in collecting. Remains of a carapace were undoubtedly destroyed. Vague traces of appendages can be seen. A long basal joint of the peduncle of both first antennae are present. Traces of their extremities are too poorly preserved for interpretation. By holding the specimen at the proper angle relative to the light source, the right exopodal scale

can be clearly seen. It is a narrow lobe fringed with setae. The other appendages are vaguely visible when the specimen is wet with alcohol. The only statement that can be made is that the remains of the thoracic legs have definite forward orientation.

Six abdominal somites constitute slightly more than one-half the body length. All are subequal in length, but they narrow posteriorly.

Wells mistook the lateral portions of the blade of the telson for the endopods of the uropods. The uropods which arise from the sixth abdominal somites have a small sympod. The sclerotized outer margins of the exopods have left clear impressions. The membranous extremity and inner margin are poorly defined. Vague suggestive remains indicate both the exopod and endopod were lobate.

The body of the telson is the best preserved and the most diagnostic portion of the fossil. It is spade-shaped with a slight convex curvature of its lateral margins. The axial ridge that extends the length of the blade misled Wells into believing that the lateral portions were the endopods of the uropods. He interpreted only the arched base upon which the intestinal filling terminates as the telson. Inward from the lateral margins are strengthening ridges. These diminish in height but increase in width posteriorly. They originate near the basal margin of the telson and extend for three-fourths of its length. At their distad termination, the ridges have arched somewhat inwardly. Indeterminate remains posterior to the body of the telson are probably vestiges of the furcal elements. They seem to have been lobate.

Synopsis.—The eumalacostracan nature of the above described remains cannot be doubted. Being from the Middle Devonian, this is the most ancient record of this taxon from North America.

Lack of a carapace on the fossil is negative evidence and proves nothing. The general appearance of the remains is that of a caridoid crustacean. No syncarid is known with the thoracic endopods normally disposed in a forward arrangement; moreover, the relatively large size of the telson negates such a taxonomic assignment.

The genus is characterized by the shape of its large telson. In *Devonocaris destinezi* (Van Straelen), the distal extremity of the telson is narrower than at its base, whereas on *D. cuylereensis* the widths are equal.

Stratigraphic occurrence.—Windon member of Moscow formation, two feet below base of Tully limestone, Hamilton group, Tioughniogan stage (Givetian stage of Europe). Middle Devonian.

Locality.—Quarry 1.5 miles northwest of DeRuyter, Madison County, New York.

Collector.—J. W. Wells.

Type.—Holotype, Cornell University, No. 40020.

SPECIES WITHOUT CARAPACE

The only fossil Malacostraca from strata of North America previously correctly interpreted as lacking a carapace are *Acanthotelson stimpsoni* and *Palaeocaris typus*. Though hundreds of excellent specimens representing both of these species are present in museum collections, these Crustacea from the Pennsylvanian Mazon Creek nodules of Illinois are poorly known. Rare specimens of *Palaeocaris* are also known from the Pennsylvanian of Nova Scotia. *P. novascotica* (Copeland, 1957 a), a Mississippian species from Canada, has a short carapace and has been redescribed herein as *Acadiocaris novascotica*. The alleged Devonian species, *P. cuylerensis* Wells (1957), is the type species of a new caridoid genus, *Devonocaris* (Brooks, 1962 a). *Belotelson*, a prawnlike Pennsylvanian crustacean, likewise has been discussed with the eumalacostracans with a carapace. On the other hand, *Squillites*, an alleged Mississippian stomatopod, is a true syncarid and will be described below.

Misconceptions of the morphology of the Paleozoic syncarids have been perpetuated for nearly a century. The taxon Syncarida was originally proposed as a suborder on the basis of Packard's (1886 a) study of *Acanthotelson*. At the time of Meek and Worthen's last study (1868 b) and Packard's revision, the most closely analogous Recent Crustacea known were the isopods and amphipods. The principal diagnostic characteristic of *Acanthotelson*, and thus the Syncarida, as presented by Packard was loss of the first thoracic tergite through fusion. This error has remained uncorrected until now. With the discovery of the Recent "Tasmanian mountain shrimp", *Anaspides*, which has the first thoracic somite fused with the head, Calman (1896) established the Syncarida as an order.

Related Recent forms have been discovered and the taxonomic category redefined to also include the fossil and extant genera with eight thoracic tergites. It is interesting that *Acanthotelson*, the original syncarid, was placed in the incertae sedis in the most recent treatise on these Crustacea (Siewing, 1959, p. 102).

Acanthotelson has fallen from grace, not because it is aberrant but because of misinterpretation and ignorance. It will be discussed first because of its historical significance. It must be re-established as the basic syncarid type.

Genus **ACANTHOTELSON** Meek and Worthen, 1865

This genus is endemic to the Pennsylvanian deposits of Illinois. Its raptorial thoracic appendages and general body form are comparable to those of *Uronectes* (Text Pl. 11, fig. b), but it is readily distinguished by the shortness of the sixth abdominal somite and by the styliform rami of its uropods and its hastate telson.

Three restorations of this genus have been published. They were drawn by Meek and Worthen (1868 b), Packard (1886 a) and Fritsch (1901). The first was the most accurate, but even this did an injustice to these remarkable fossils. Dorsal, ventral, and lateral views have been drawn (Text Pl. 10, Text Pl. 11, fig. a) of *Acanthotelson stimpsoni* based upon knowledge gained from this study.

The genus is monotypic being represented only by *A. stimpsoni*. All specimens are from Mazon Creek nodules. Over 1200 individuals are now present in various museum collections making this the most abundant fossil malacostracan to be found in this or any other Paleozoic deposit.

Acanthotelson stimpsoni Meek and Worthen, 1865 Pls. 54-59,
Text Pl. 10; Text Pl. 11, fig. a

Acanthotelson stimpsoni Meek and Worthen, 1865, p. 47.

Acanthotelson stimpsoni, Meek and Worthen, 1866, p. 401-404, pl. 32, figs. 6, 6 a-f.

Acanthotelson eveni Meek and Worthen, 1868 a, p. 27.

Acanthotelson stimpsoni, Meek and Worthen, 1868 b, p. 549, fig. 1.

Acanthotelson eveni, Meek and Worthen, 1868 b, p. 551, 4 figs.

Acanthotelson stimpsoni, Brocchi, 1880, p. 10, pl. 1, fig. 11.

Acanthotelson stimpsoni, White, 1884, p. 176-177, pl. 37, figs. 4, 5.

- Acanthotelson eveni*, White, 1884, p. 177-178, pl. 38, figs. 4-7.
Acanthotelson stimpsoni, Packard, 1886a, p. 123-127, pl. 1, figs. 1-3; pl. 2, figs. 1-3.
Eileticus anthracinus Scudder, 1890, p. 420-421, pl. 38, fig. 5.
Eileticus aequalis Scudder, 1890, p. 421, pl. 38, figs. 6-9.
Acanthotelson stimpsoni, Calman, 1896, p. 799, pl. 2, fig. 16.
Acanthotelson sp. Fritsch, 1901, p. 74, fig. 398.
Acanthotelson stimpsoni, Smith, 1909, p. 575, fig. 62.
Acanthotelson stimpsoni, Vanhoeffen, 1916, p. 146, fig. 12.
Acanthotelson eveni, Vanhoeffen, 1916, p. 148.
Acanthotelson sp. Vanhoeffen, 1916, p. 148, fig. 14.
Eileticus aequalis, Pruvost, 1919, p. 89-91, fig. 23.
Acanthotelson eveni, Van Straelen, 1931, p. 11-12.
Acanthotelson stimpsoni, Van Straelen, p. 12.
Eileticus aequalis, Vandenbergh, 1960, fig. 1 b.

Meek and Worthen established three species. They are: *Acanthotelson stimpsoni* (1865), *A. inaequalis* (1866) and *A. eveni* (1868 a). Packard synonymized *A. eveni* believing that these larger more robust individuals were adults of *A. stimpsoni*. Most authors have been unaware that *A. inaequalis* is equivalent to *Palaeocaris typus* Meek and Worthen. Not only does Vanhoeffen (1916) redefine all three species, but one additional species, based on an inaccurate restoration by Fritsch (1901), is recognized but left unnamed. Though closely related species do sometimes exist in the same ecological niche, it is the exception. Especially in paleontology, one must be cautious in recognizing sympatric species. Though the statistical analysis of the size of the individuals (Text Pl. 12, fig. c) of the population is not a typical distribution, it shows a continuum and there is absolutely no morphological basis for justifying differentiation of the larger individuals as belonging to a separate species.

Description of specimens.—The holotype, UI X-346 (ISMNH 1118) (Pl. 54, fig. 4) is in the collections of the University of Illinois. Another specimen designated as the type of *A. eveni* (UI X-344) is the result of a curatorial error.

Four hundred twenty-three specimens of *Acanthotelson stimpsoni* were prepared and studied in detail. An additional 792 specimens in the S. S. Strong collection were superficially examined for features not present on those already studied. All occur in ironstone concretions from Mazon Creek and the adjoining strip mines in Grundy and Will counties, Illinois.

Of the specimens that have been collected, about fifty percent are large, robust individuals of the type previously termed *A. eveni*. Meek and Worthen were impressed in the original study by the fact that all specimens were lateral compressions. This was fortuitous. Sixty-three percent of the population sample now known are oriented in a dorsal-ventral position with their pereopods outspread.

Some of the larger individuals of this species retain much of their original relief; however, many specimens are badly compressed. From this it may be presumed that the chitinous exoskeletons of the larger individuals were strong; however, there is no evidence of fortification with mineral matter. In all specimens the surface texture of the skeletal elements is smooth. Impressions of bristles, spines, and setal sockets are commonly preserved on the appendages.

Three divisions of the body can be distinguished. There are no rudiments of a carapace. Previous observations to the contrary, all eight thoracic somites are separate and distinct. Thus the cephalic tagma bears a pair of stalked compound eyes and five pairs of appendages, the first antennae, second antennae, mandibles and two pairs of maxillae. The thorax consists of eight distinct somites each of which bears a pair of appendages. It is known that the last six pairs are biramous. The six abdominal somites bear biramous appendages of which the last pair are modified as uropods. The telson lacks any trace of furcal rami.

Only the combined length of the head and thorax, exclusive of rostrum, and the body length, exclusive of rostrum and telson, could be measured with enough accuracy to merit mathematical analysis. However, measurements of the length of the rostrum, length of head exclusive of rostrum, length of thorax, length of abdomen, and length of the telson and body length are presented for the holotype and other representative specimens (Text Pl. 11, fig. c).

The length of the body was determined on all specimens whereon this measurement could be made or estimated with reasonable accuracy. When these data were plotted graphically, a binodal curve was obtained suggesting a composite of two population samples with modes at 22 mm. and 33 mm. It was noticed that larger individuals were considerably more abundant in all but the S. S. Strong col-

lection at Yale. A random sample of 216 specimens from this collection was used as the most representative sample of the population not prejudiced by a collecting factor, since Strong was paid for each specimen irrespective of size and preservation. Using this sample, a reasonably normal curve for the size frequency was obtained (Text Pl. 12, fig. c). It has the following values: Max = 55 mm., Min = 12 mm., Mo = 28 mm., Me = 28 mm., Ma = 29 mm., and a standard deviation of 8 mm.

The size frequency of the population is unusual in the abundance of individuals larger than the mode. Two percent are twice as large. The great range in size is disturbing, but we must not be misled into believing the species is dimorphic or that two species are represented. These hypotheses were thoroughly tested statistically and by careful scrutiny of the specimens for distinguishing criteria before they were abandoned. Though data are not available on undisturbed populations of the American lobster, *Homarus americanus*, it is known that some individuals attain gigantic size relative to those commonly caught. It is believed *A. stimpsoni* had a comparable longevity. Thus the size frequency distribution of the population is of paleocological not taxonomic significance.

The combined length of the head and thorax is greater than that of the abdomen. Forty-five observations of the ratio of the combined length of head and thorax to body length (less telson) gave the following values: Mo = 0.60, Me = 0.59, Ma = 0.59 and S = 0.04.

Compared to other Crustacea the head of *A. stimpsoni* is relatively small. Though it represents five fused appendages bearing somites, its length is slightly less than one and one-half the length of the typical thoracic somite.

The dorsal cephalic shield is well preserved on many specimens (MCZ 5210, Pl. 55, fig. 1; PY 19842, Pl. 56, fig. 1, and PY 19902, Pl. 57, fig. 3). It is less well preserved on those specimens that are lateral compressions. The lateral restoration (Text Pl. 11, fig. a) is based principally on PY 19834, PY 19849, PY 19867, and PY 19835. The cephalic shield is produced mid-dorsally into a small triangular rostrum as shown on PY 19902 (Pl. 57, fig. 3). Other specimens on which the complete rostrum remains are PY 19644,

PY 19692, PY 19842, PY 19844, PY 19877, PY 19878 and PY 19904. From these, it appears to be about one-fifth the length of the head. Two transverse grooves divide the shield. The anterior groove crosses the dorsal portion of the shield whereas the posterior groove is divided into two separate parts. From its dorso-lateral origins at the posterior of the head, it extends forward on either side for about one-third the length of the cephalon. It then follows a course obliquely downward terminating anterior to the mandible articulation (PY 19842). This is the cervical groove. The anterior and posterior grooves merge just above the mandibular articulation. Posterior to this position, the depth of the head becomes equal to that of the succeeding somites. A narrow flange borders the cephalic shield on its ventral and anterior margins and extends onto the rostrum.

The eyes and cephalic appendages are exceptionally well preserved on some of the specimens, however, ventral views of the head structure are poor. The foramina for the eyes and, in some cases, for the antennae can be seen on the epistome (PY 19842, Pl. 56, fig. 1). The simple epistome posterior to the foramina for the second antennae is preserved on PY 19839 (Pl. 57, fig. 2). This specimen also shows the mandible articulation. If remains of a labrum exists on any of the specimens it is the triangular process anterior to the mandibles on PY 19854 (Pl. 59, fig. 1).

Stalked compound eyes extend from their base beneath the rostrum. Many specimens display one or both of the eyes and they are present on specimens studied by Meek and Worthen and by Packard. They failed to recognize them on their unprepared specimens. Even the faceted cornea is preserved on PY 19902 (Pl. 57, fig. 3).

The symphods of the first pair of antennae are also well displayed on this specimen. The three joints are even better preserved on PY 19842 (Pl. 56, fig. 1). Setal sockets on the inner margins of all three joints can be seen on PY 19842 (Pl. 56, fig. 1) and PY 19854 (Pl. 59, fig. 1). On the distal joint the row of setae are small and close together. The second joint had four or five larger setae and there were five or six on the basal joint. The annulate rami are both present on PY 19903, PY 19713, and PY 19906. The outer

flagellum, the exopod, is about one-third the length of the body (11 mm. / 33.4 mm. on PY 19887 and 10 mm. / 34 mm. on PY 19904) and is composed of approximately 54 annuli. On PY 19842 the small inner flagellum is 4.5 mm. long and is made up of 18 annuli. The endopod is approximately one-third the length of the outer flagellum or equal to one-ninth the length of the body of the animal.

The endopod of the second antenna has three basal joints and a long flagellum. Such endopods are present on many specimens but are particularly good on MCZ 5210 (Pl. 55, fig. 1). The flagellum is nearly as long as the length of the body and telson combined. It appears normally to have been trailed lateral to the body. Setal sockets can be seen on all three of the massive basal joints on PY 19854 (Pl. 59, fig. 1). The antennal sympod seems to have been reduced to a single joint. It is the second joint of the sympod which is produced as a stipe for the antennal scale that is usually preserved on the other species. No trace of this joint or the exopod was detected. A single, short, robust sympodal joint is readily distinguished on PY 19867 (Pl. 59, fig. 6). On the ventral side of the example mentioned, a prominent nephropore is present. In all other syncarids known, the excretory glands are associated with the second maxillae on the adult animals.

The mandibles are unusually massive with a strong incisor lobe, vide PY 19839 (Pl. 57, fig. 1). The body of the mandible had only one articulation. The extended condyle articulated with the exoskeleton of the head just posterior to the cervical groove (PY 19839, Pl. 57, fig. 2). From the broad anterior bench on the body of the mandible a palp originated. The basal joint of this structure is preserved on PY 19725, PY 19664 and PY 19867 (Pl. 59, fig. 6). The longer second joint of both the left and right palp is preserved on PY 19854 (Pl. 59, fig. 1).

A lobate structure between the mandible and the first maxillae can be seen on PY 19839 (Pl. 57, fig. 1). This may be one of the paragnaths.

The two pairs of maxillae can be distinguished only on the laterally oriented specimens. A three-jointed endopod of the first maxillae can be seen on PY 19835 and PY 19839 (Pl. 57, fig. 1).

The only relic of the second maxillae is the basal joint of the endopod on PY 19839. A three-jointed endopod is not uncommonly retained on the second maxillae of the lower Eumalacostraca, but it is unusual for it not to be aborted on the first. The endites which are always the most conspicuous elements of the maxillae on Recent Malacostraca are unknown in this genus.

Both Meek and Worthen and Packard interpreted the thorax as having only seven tergites. They overlooked the first tergite which is reduced to a narrow collar overlapping the posterior border of the head (MCZ 5210, Pl. 55, fig. 1; PY 19902, Pl. 57, fig. 3). The next three tergites are progressively larger and the last four are of equal size. The fourth tergite, which is the longest, overlaps both anteriorly and posteriorly. A ridge borders the anterior portion of each of the last four tergites which imbricate posteriorly. The surface of the exoskeleton is smooth, and there are no spines or processes. Even the pleural borders are not developed; they are abruptly truncated.

The sternites were observed only on PY 19847 (Pl. 59, fig. 3). These sclerites are greatly reduced. However, there are wide flanges or epemera between the legs and tergite. This is best seen on PY 19846.

The last five pairs of thoracic appendages were equally developed whereas the first are greatly reduced and the endopods of the second and third are modified as large raptorial structures. All except the single small pair of maxillipeds are displayed by PY 19867 (Pl. 54, fig. 3). The normal stance was with the pereopods extended laterally (MCZ 5210, Pl. 55, fig. 1, PY 19744, Pl. 58, fig. 1) and the raptorial appendages extended forward (PY 19842, Pl. 56, fig. 1).

The typical biramous pereopod has a sympod of two joints, lobate exopod and epipods, and a five-jointed endopod. The coxa and basis of the sympod are shown on PY 19854 (Pl. 59, fig. 1), but their existence is definitely proven by PY 19707 (Pl. 58, fig. 3), PY 19867 (Pl. 54, fig. 3), MCZ 5233, and PY 19875.

Laminate blades are associated with the thoracic appendages (PY 19884, Pl. 59, fig. 9). It can be seen that most of these are exopods (PY 19640, Pl. 55, fig. 2). A flagellum does not exist. What

appears to be annuli on some specimens is the margin of the exopod blade divided by setal sockets. This interpretation is verified by PY 19839. The exopod blade has a short stalk and articulates with the basis. The six posterior thoracic appendage (PY 19711 and PY 19640) are biramous and it is probable the two preceding were likewise.

There appears to be more than one blade per appendage on PY 19884 and PY 19640 (Pl. 55, fig. 2). We may be seeing left and right exopods; however, since they are of unequal size it is believed the extra lamellae are epipods which arose from the coxa.

The endopods are shown in the photographs of PY 19867 (Pl. 54, fig. 3) and PY 19744 (Pl. 58, fig. 2). The small terminal dactylus can be seen on PY 19744 and PY 19707 (Pl. 59, fig. 5). Setal sockets are present on the joints of the endopod of these specimens. Bristles on the carpus and merus are best seen on PY 19849. The "knee" of the five-jointed endopod is between the merus and carpus.

The second pair of thoracic appendages were modified as large raptorial legs (USNM 38845, Pl. 54, fig. 2). The third pair is intermediate in size but is also raptorial (PY 19813, and PY 19842, Pl. 56, fig. 1). They are known to be biramous. The dactylus of both pairs of appendages has heavy curved spikelike claws (PY 19844, Pl. 54, fig. 1; MCZ 5224, Pl. 59, fig. 7). The two distal claws are much longer and stouter than the other five. The propodus and carpus also had spines (PY 19744, Pl. 58, fig. 2). These are reduced to heavy bristles on the third pair of appendages.

Evidence of the first pair of thoracic appendages is uncertain, but joints of a small appendage are present on PY 19653 (Pl. 59, fig. 2) and MCZ 5210. It is believed the endopod retained five joints.

Only two things were learned of the internal anatomy from the fossils. From the position of nephropores on the second antennae, the position of the excretory glands is established and a detrital filling of the intestinal tract on one specimen (PY 19744, Pl. 58, fig. 2) shows a simple stomach and intestine.

No sexual differences were detected.

All six of the abdominal somites are subequal in length. In other fossil syncarids the pretelson somite is considerably longer than the others. Many of the fossils have the tergites of the abdomen

spread more than the thoracic tergites, *i.e.*, MCZ 5210 (Pl. 55, fig. 1). This is due to their greater depth because of the development of pleural lobes. The abdominal somite actually tapered in width posteriorly.

The typical abdominal tergite does not differ significantly from those of the thorax in dorsal aspect (PY 19842, Pl. 56, fig. 2). A lateral bulge acting as a fulcrum between the tergites is conspicuous on the last thoracic somite as well as those of the abdomen. The pleural lobes are, however, distinctive. The ventral margins of the plates are curved throughout, but the arc of least radius is posterior. The posterior marginal arc is armed with five spines with the ventral spine the most strongly developed. The posterior margin of the fifth abdominal tergite is serrated completely across. Unusually large spines rise above the dorsal articulation of the sympods of the uropods with the sixth abdominal somite (Pl. 55, fig. 1). The mid-dorsal posterior margin of this tergite bears eight denticles arranged in a central group of four separated by a gap from two lateral denticles. The main body of this somite narrows to the width of the telson; however, the width of the flanks is maintained to accommodate the sympods of the uropods.

The sternites of the five anterior abdominal somites are relatively wide. The foramina on the sclerites for the appendages are large. Though not shown by the photograph of PY 19817 (Pl. 59, fig. 4), there is a bridge posterior to the insertion of the appendage. The sternite of the pretelson somite covers nearly its complete ventral surface (PY 19866).

Many specimens have traces of swimmerets, but they are rarely well enough preserved for structural interpretation. The single jointed sympods for all five of the left appendages are present on PY 19692. These and the poorly preserved rami can be seen on all but the first abdominal somite of PY 19867 (Pl. 54, fig. 3). The outer and inner branches are both unjointed laminae. The bladelike exopod shown on PY 19846 (Pl. 59, fig. 8) is setiferous on the straight outer margin as well as on the thinner curved inner edge. The restorations of Meek and Worthen and of Packard show the wrong proportional development. The rami of the swimmerets are at least four times longer than the short, stout sympod. The rami are definitely not annulate as shown by Fritsch.

The uropods provide the most distinctive characteristic of this genus. The single jointed sympod articulated dorsally and ventrally with the sixth abdominal somite such that these appendages could be moved only laterally. Both rami are reduced to long, curved, slender blades. The inner blade is more strongly arched near its tip. Being thin, both branches are strengthened dorsally and ventrally by raised medial ridges. The total length of the uropods is equal to that of the telson or one-fourth of the length of the body of the animal.

The uropods are well preserved on MCZ 5210 (Pl. 55, fig. 1). Both branches are setiferous. Except for the inner margin of the exopods, the setal rows are interrupted by stout spines. These stout bristles are equal in length to the fine setae. Eight to ten setae are present between each spine (PY 19842 and PY 19653).

From an arched broad base the telson becomes a thin, narrow spike. The spikelike terminal three-fourths of the telson is strengthened by a mid-dorsal ridge. Its borders are armed with spines and setae arranged as on the branches of the uropods.

Synopsis.—Only one species of *Acanthotelson* can be distinguished in the population sample from the Francis Creek shale at Mazon Creek and the adjacent strip mines. Most of the external morphology of this crustacean is now known and has been presented in the restorations. In common with *Uronectes*, it has raptorial appendages but is easily distinguished by the shortness of the sixth abdominal somite and the styliform uropods and telson. Of great phylogenetic significance is the discovery of a nephropore on the basal joint of the second antennae.

Stratigraphic occurrence.—Francis Creek shale, Carbondale formation, Alleghany Series (Westphalian), Pennsylvanian in the Mazon Creek nodules.

Localities.—Grundy and Will counties, Illinois.

Collections.—The best collection is the S. S. Strong collection at Yale University. Other collections are in the Chicago Museum of Natural History, Illinois State Museum, U.S. National Museum and the Museum of Comparative Zoology.

Types.—The holotype is in the University of Illinois collection, X-346 (ISMNH 1118). All of the plesiotypes figured by Packard are

in the collection of the United States National Museum, USNM 38845.

Genus **PALAEOCARIS** Meek and Worthen, 1865

This genus was established upon specimens from the Pennsylvanian deposits at Mazon Creek, Illinois. The type species, *Palaeocaris typus*, was described by Meek and Worthen (1865, 1866 and 1868 a, b) and was re-described by Packard (1886 b). Despite the studies of these distinguished paleontologists, the only reliable morphological description of this genus is by Calman (1911 b, 1932 a) based upon closely related species from England, *P. praecursor* (Woodward) and *P. retractata* Calman. His limited materials were inadequate for accurate interpretation of several morphological features.

Restorations of *Palaeocaris typus* have been attempted by Meek and Worthen (1868 b) and by Packard (1886 b, pl. 3, fig. 1). The restorations presented herein (Text Pl. 13, Text Pl. 12, fig. a) illustrate all morphological characters seen on the fossils.

The most distinctive characteristics of the genus are as follow: the first five thoracic tergites are imbricated forward, the large sixth tergite overlaps both adjoining tergites, the last two tergites imbricate posteriorly, and pleural lobes are present on these as well as on the abdominal tergites. The rami of the uropods are lobate blades. The endopod is three-fourths as long as the exopod. The telson is spatulate. The caudal fan of *Uronectes* is similar, but this genus is readily distinguished by a pair of large thoracic raptorial appendages. The pereopods of *Palaeocaris* are unusually long and slender. The first pair is reduced. These and other morphological features will be clarified with reference to the large number of specimens of *P. typus* now available.

Palaeocaris typus Meek and Worthen, 1865

Pls. 60-64; Text Pl. 12,
fig. a; Text Pl. 13

Acanthotelson inaequalis Meek and Worthen, 1865, p. 48.

Palaeocaris typus Meek and Worthen, 1865, p. 49.

Acanthotelson inaequalis, Meek and Worthen, 1866, p. 403, p. 32, fig. 7.

Palaeocaris typus, Meek and Worthen, 1866, p. 405, pl. 32, figs. 5, 5a-d.

Palaeocaris typus, Meek and Worthen, 1868 a, p. 28.

Palaeocaris typus, Meek and Worthen, 1868 b, p. 552, 2 figs.

- Palaeocaris typus*, Brocchi, 1880, p. 9, pl. 1, figs. 8-10.
Palaeocaris typus, White, 1884, p. 179-180, pl. 38, figs. 1-3.
Palaeocaris typus, Packard, 1886 b, p. 129-133, pl. 7, figs. 1-2.
Palaeocaris typus, Packard, 1889, v. 24, p. 213.
Palaeocaris typus, Calman, 1896, p. 796, p. 2, fig. 15.
Palaeocaris typus, Smith, 1909, p. 570, text figs. 56-58.
Palaeocaris typus, Vanhöffen, 1916, p. 141, fig. 5.
Acanthotelson inaequalis, Vanhöffen, 1916, p. 147.
Palaeocaris typus, Siewing, 1959, p. 100.
Palaeocaris typus, Rolfe, 1962, p. 548-549.

Palaeocaris typus is a synonym of *Acanthotelson inaequalis*. Through the latter has page priority, Meek and Worthen suppressed it in favor of *P. typus* upon which the genus was described (1868 b, p. 562, footnote). Because the name *A. inaequalis* has never been used correctly and *P. typus* is an established name, the decision of the first revisor should be accepted. The species is characterized by having no transverse striae on its thoracic and abdominal tergites and by the presence of small spines completely across the posterior margins of all abdominal tergites.

Description of specimens.—Two hundred eighty-six specimens of *Palaeocaris typus* from the Mazon Creek nodules were prepared. An additional 482 specimens were given cursory examination to discover features not previously discovered on the prepared specimens. For morphological study, the best specimens are in the collections of the Peabody Museum, Yale University, the U.S. National Museum, and the Museum of Comparative Zoology.

Holotypes of *Acanthotelson inaequalis* and *Palaeocaris typus* figured by Meek and Worthen have not been located. They may ultimately be discovered in the collections of the Illinois Geological Survey or the University of Illinois. The 12 plesiotypes studied by Packard are in the collections of the U.S. National Museum. The best specimen is refigured herein (USNM 38850, Pl. 62, fig. 2).

MCZ 5192 and CMNH 29405 are the only specimens that have retained their original relief. All other specimens are deformed by compression (PY 19731, Pl. 63, fig. 1). The chitinous exoskeletal sclerites were undoubtedly much less firm than those of the associated crustacean species. The original skeletal material has disintegrated. Unless otherwise indicated, the descriptions and photographs are of rubber molds of the natural impressions.

The surface texture of the exoskeleton was completely smooth. The fine spines across the posterior margin of the abdominal tergites are the only skeletal frill. The appendages and telson were setiferous.

The majority of the specimens are lateral compressions. This contrasts with the preferential dorsal-ventral orientation of *Acanthotelson*.

The three primary divisions of the body are the head, thorax, and abdomen. Eight separate thoracic somites are present; however, the tergites and appendages of the first are reduced. The head has prominent stalked compound eyes and consists of five fused appendages bearing somites. There is no rudiment of a carapace. The abdomen consists of six somites and a simple, flattened, spatulate telson. The most conspicuous body division back of the head is at the sixth postcephalic somite from which the tergites overlap toward either extremity.

The small size of the individuals and state of preservation make it impossible to obtain precise measurements for statistical analysis for all but the length of the body less the telson. It was found the most reliable relationships could be determined on a few select specimens. For example, the length of the head and thorax to the body length as defined above was consistently 0.58 on the specimens on which these measurements could be most accurately determined. On the other specimens there was a great range in this proportion. By selecting the best fossils for measurements, a statistical error is avoided. Measurements of representative specimens are presented in Text Plate 11, figure c. Where pertinent, proportions will be presented in the morphological description.

The size frequency distribution within the sample is shown graphically in Text Plate 12, figure b. The maximum size was 35 mm. and the minimum size was 12 mm. The median and mode are at 22 mm. The distribution is skewed toward the upper sizes. This is normally exhibited by fossil populations. The standard deviation of 4.5 mm. about the arithmetic mean of 21 mm. reflects a strong central tendency.

The cephalic tagma of five fused somites is the same length as the sixth thoracic tergite and the sixth abdominal tergite. Each contributes one-ninth of the length of the body.

The dorsal cephalic shield is undivided dorsally (CMNH 29405, Pl. 61, fig. 1), but a shallow groove arises on the sides just anterior to the mandibles. It diminishes upward and no trace is to be found beyond a faint longitudinal groove. This groove arises at the posterior margin of the shield (MCZ 5197, Pl. 60, fig. 2). The cephalic shield attains the full depth of the body posterior to the mandibular groove. It rapidly diminishes in depth anteriorly with its ventral edge facing forward at an angle of about forty-five degrees to the axis of the animal's body. An antero-lateral angle of about 90 degrees is formed by an abrupt curvature of the margin of the shield. What is equivalent to the anterior margin in other syncarids is recessed through a broad arc to form a large orbital notch. Between the orbital notches, the carapace projects slightly forward as a truncated plate. This supraorbital plate is strengthened at either side, but it is not developed as a typical rostrum (CMNH 29405, PY 19767 and PY 18823).

A bridge of the epistome projects forward of the dorsal shield below the foramina for the eyes (CMNH 29405, Pl. 61, fig. 1). This condition is unknown in other adult syncarids but is recapitulated in the development of the stalked eyes of *Anaspides tasmaniae* (Thomson) (Hickman, 1937, p. 24, pl. 6, figs. 40-43).

Eye stalks are present on PY 18850, PY 19715, PY 19731 (Pl. 63, fig. 1), PY 19736, PY 19750, PY 19795, PY 19812, PY 19823 (Pl. 63, fig. 2), and USNM 38851-404f. The peduncle is short and stout. This accounts for the large ocular orbit. An unexpected feature is the prominent peracarid-like papillae clearly present on both eye stalks of PY 19823 (Pl. 64, fig. 5). Its existence is further validated on PY 19765. The cornea of the eye was not seen.

Both pairs of antennae are articulated ventral to the epistomal bridge. A strongly sclerotized plate between the first antennae is preserved on many specimens, *i.e.*, PY 19775 (Pl. 61, fig. 3), PY 19783 (Pl. 62, fig. 3), and USNM 38851-404p (Pl. 62, fig. 1). This sclerite is a distinct division of the epistome. As in some of the other primitive Eumalacostraca, it is interpreted as a rudiment of the sternite of the first antennal somite. The ventral skeletal portion of the epistome associated with the second antennae is poorly preserved on USNM 38851-404p. The mouth is shielded anteriorly by a sclero-

tized labrum which is expanded near its extremity (PY 19812, Pl. 61, fig. 4), much like that of *Anaspides*.

Remnants of the first antennae are present on a great many specimens. The three-jointed sympod is best preserved on PY 19783 (Pl. 62, fig. 3; Pl. 64, fig. 3). The stout basal joint is equal to the combined length of the other two joints. The terminal joint is only slightly longer than the second. Two rows of setal sockets are present on the basal joint of PY 19783 (Pl. 64, fig. 3). Setae can be seen on the second and third joints of this specimen. Portions of both flagella are present on several specimens. The length of the inner flagellum is about one-fifth the length of the body of the animal. It is believed that the other flagellum was about a third the body length (PY 19736 and PY 18917).

Despite the excellent preservation of portions of the second antennae on PY 19812 and PY 19783, the basal joint is unknown. The endopod arises near the base on the mesad side of a large joint that extends as a stipe for the antennal scale. By homology, this joint is the second joint of the sympod. Though a careful search was made, the first joint was not seen on any of the fossils. The exopod is a lobate squama. Its outer margin is not produced as a spine, but is slightly convex and bears setae as does the curved inner margin and broadly rounded tip. Three joints of subequal length and a long flagellum form the endopod. Setae on the mesad side of these joints can be seen on PY 19783 (Pl. 62, fig. 3). The length of the flagella of this pair of antennae is equal to the body length (PY 19705).

The mandible articulates with the cephalic shield posterior to the cervical groove (MCZ 5197, Pl. 60, fig. 2). Though the body of the mandible is large, it is not so stout as that of *Acanthotelson*. As in the Recent *Anaspides*, the shoulder anterior to the incisor lobe was the site of origin of a palp. The short isolated joint seen on PY 19775 (Pl. 61, fig. 3) is the same shape as the basal palp joints observed on *Acanthotelson*. The longer second joint is known (PY 19812, Pl. 61, fig. 4).

The basal joint of one of the first pair of maxillae is well preserved on PY 18855 and is identical to those seen on specimens of *A. stimpsoni*. The terminal joint is only poorly preserved on PY 19786, but there is a good ventral view of two joints of the second

maxilla. The lateral compression of PY 19755 (Pl. 62, fig. 4) has remains of both pairs of maxillae preserved. The ventral skeletal sclerite supporting these appendages is shown by USNM 38851-404 p (Pl. 62, fig. 1).

Though the first thoracic somite is greatly reduced in length, all eight tergites remain freely articulated. Somites two through eight are subequal in length as shown by the margin of the tergites; however, they appear unequal dorsally because of imbrication. Mid-dorsally the sixth tergite is twice as long as the typical somite. This is because it overlaps both anteriorly and posteriorly. Tergites anterior to this imbricate forward. The first forms a collar extending upon the head shield. All tergites succeeding the sixth articulate in the normal manner.

The pleural lobes of this genus provide a distinguishing criterion that can be seen on most of the fossils. The anterior margin of the tergite gives way to the free pleural lobes through a broad arc. The posterior margin remains nearly straight. At the intersection of these edges the apex of the pleural plate is blunted (PY 19755, Pl. 60, fig. 1).

At least seven of the thoracic legs were biramous and there is definite proof of epipods. All endopods except the first are not uncommonly preserved (PY 19731, Pl. 63, fig. 1). There are five joints. The knee is between the merus and carpus. The pereopods are slender. Successive pairs increased slightly in length posteriorly. The two joints of the sympod can be seen on USNM 38841-404. These and the ischium are particularly good on PY 18858 and PY 19750 (Pl. 60, fig. 3).

The blades of the exopod with their peduncle are present on many specimens (vide PY 19765, Pl. 63, fig. 4; MCZ 5197, Pl. 60, fig. 2; Pl. 62, fig. 6). Evidence of the setae which originally fringed the blades can be seen on these specimens in the form of setal sockets. Packard thought the exopods were jointed and Calman mistook the setal sockets for sutures of annuli. Seven exopods are preserved on both sides of USNM 38851-404. The exopod of the first thoracic leg is unknown.

The exopod arises from the basis. A tubular structure which must be the base of an exipod is seen to originate on the basal joint,

the coxa, of the sympod above the exopod on the seventh thoracic appendage of PY 19731. Similar tubular structures are present on PY 19779, PY 19781 (Pl. 62, fig. 5), PY 19783, and PY 19765 (Pl. 63, fig. 4). On PY 19756 stalks are present above the exopods on both the seventh and eighth thoracic appendages. The lamellae of the exipods were not preserved. This would be expected if their integument was as thin as on the Recent syncarids. On *P. typus* the exopods extend between the pleural lobes of the tergites. It is probable that the sclerotized cylindrical stalks developed because of this.

This first pair of thoracic legs is reduced to less than half the size of the succeeding legs. Some of the joints can be seen on PY 19858, PY 19766 and USNM 38851-404f. The merus on PY 19755 (Pl. 62, fig. 4) is about half the length of the homologous joint on the normal pereopod.

The thoracic sternites were nearly as long as their somites. Foramina for the legs are set wide apart leaving a more heavily sclerotized central plate. They are ornamented mid-ventrally by a small mound (PY 19775).

Detrital intestinal fillings are common on the fossils of this species. Fossils of *P. typus* are distinguished by impressions of longitudinal striations which reflect a ridge and groove structure of the interior of the intestine (PY 19750, Pl. 60, fig. 3). Some of the fillings extend through the thorax and abdomen into the base of the telson. The striations are restricted to internal molds of the posterior portion of the gut.

Six abdominal tergites, uropods, and the telson are present on most specimens. The first five abdominal tergites are subequal in length with pleural lobes like those of the thoracic tergites. The abdominal tergites are distinguished by a fringe of fine spines completely across the posterior border. The abdomen narrows gradually in width. The sixth abdominal tergite is slightly over half again as long as those preceding. As the main body of this somite rapidly narrows to the width of the telson, its anterior width is maintained by the development of marginal flanges. Each flange extends posteriorly beyond the main body of the somite for about one-quarter of its length. Their post-lateral angle is produced as a spine lateral to the sympod of the uropod (PY 19729, Pl. 64, fig. 4).

The ventral surface of each abdominal somite is nearly covered by a sternite. Foramina for the paired appendages are located laterally near the posterior border. Between the legs each sternite is strengthened by a slight crest (USNM 38851-404z, Pl. 63, fig. 3). The ventral sclerotized surface of the sixth abdominal somite is shown by PY 18917 and PY 19729 (Pl. 64, fig. 4). On this sternite there is a deep mid-ventral recession of the posterior edge.

Swimmerets were present on the first five abdominal somites. These can be seen on PY 19731 (Pl. 63, fig. 1). Their structure is similar to that of *A. stimpsoni*. The sympod is composed of a single stout joint (PY 19750, Pl. 60, fig. 3). It gives rise to two rami. They are blade-shaped and, as indicated by setal sockets, were fringed with setae (PY 19731, Pl. 63, fig. 1).

CMNH PE-2511 is incomparable for the preservation of the elements of the caudal fan. Both dorsal and ventral impressions make it possible to determine the true shape of both rami of the uropods as well as see the distribution of the fringing setae. Though not preserved on this specimen, the single joint of the sympod is excellent on PY 19917 and PY 19729 (Pl. 64, fig. 4). The lateral margin of the exopod is slightly convex. This sclerotized margin appears to be devoid of spines or bristles except for three terminal spines which arise anterior to the position of the transverse suture which divides the blade of the exopod. But in addition to the spines there are eight small inconspicuous bristles on the lateral margin (PY 19729, Pl. 64, fig. 4). The articulated terminal lobe is semi-circular in shape. The margin of the terminal lobe and the slightly concave inner margin of the blade are fringed with setae. From the dorsal articulation with the sympod a prominent ridge extends the length of the blade. The endopod is more lobate and its complete free margin is fringed with setae. The lateral margin is convex whereas the inner edge is nearly straight. The endopod is only three-fourths as long as the exopod. Its tip extends barely to the transverse suture on the outer ramus.

The telson is spatulate with the basal axis dorsally arched to accommodate the intestine (USNM 38851-404v). It is widest near the base beyond which it gradually narrows. The tip is broadly curved. As shown by CMNH PE-2511 (Pl. 64, fig. 1) its margin

was fringed with setae. The length of the telson on all specimens determined was equal to one-sixth the length of the body.

Synopsis.—Though the head shield is distinctive, the genus can most readily be distinguished by the shape of the pleural lobes of the thoracic and abdominal tergites, the large sixth thoracic tergite which overlaps those of both adjoining somites, forward imbrication of the first five thoracic tergites, and the shape of the blades of the uropod and the spatulate telson. Small spines are present completely across the posterior margin of all the abdominal tergites on *P. typus* and *P. praecursor* (Woodward). In both of these species the pereopods are long and slender. The tergites of *P. praecursor* are, however, transversely striated. Species that might be confused with *P. typus* are *P. vandergrachtii* Pruvost (1922, p. 147-150) and *P. retractata* Calman (1932 a, p. 541), but these do not have the spinose frill on the abdominal tergites.

Stratigraphic occurrence.—Francis Creek shale, Carbondale formation, Alleghany series (Westphalian), Pennsylvanian in Mazon Creek nodules.

Localities.—Grundy and Will counties, Illinois.

Collections.—The largest collection is in the Peabody Museum, Yale University. Other large collections are in the U.S. National Museum, Chicago Museum of Natural History, and the Museum of Comparative Zoology.

Types.—Holotypes of *P. typus* and *Acanthotelson inaequalis* are misplaced or lost. Packard's (1886 b) 12 plesiotypes are in the collection of the U.S. National Museum, 38850.

***Palaeocaris canadensis*, new species**

Pl. 65, figs. 1, 2

Palaeocaris sp. Copeland, 1957 a, p. 595, pl. 67, fig. 5.

Palaeocaris cf. *typus* Meek and Worthen, Copeland, 1957 b, p. 47, pl. 15, fig. 1

Counterparts of an excellent specimen in the Museum of Comparative Zoology, MCZ 5435, represent an unnamed Pennsylvanian syncarid from Canada. In that Copeland has previously identified the specimen as *Palaeocaris typus*?, the characterless specimens figured by him are herein considered to be synonymous.

All the basic morphological elements that can be determined on the Canadian specimens have their counterpart on *P. typus*. Whereas *P. typus* is without ornamentation of any nature on the thoracic tergites, the new species has two pronounced transverse grooves on each tergite, thoracic as well as abdominal. These markings are readily distinguished from the features resulting from compression of the imbricated margins of the tergites. Transverse ornament is characteristic of many of the Paleozoic syncarids. Two other species of *Palaeocaris* are so distinguished. *Palaeocaris burnetti* Woodward (1881) has eight to ten subparallel striae crossing each tergite from side to side and *P. praecursor* Woodward (1908) has three to four.

Description of specimen.—The fossil is preserved as a compression of low relief in black shale. One counterpart is negative impression; the other retains the carbonized remains of the chitinous exoskeleton. The specimen is broken, and the abdomen beyond the second tergite was not collected. The combined length of the head and thorax is 7.8 mm. With the same body proportions as *P. typus*, the body length of the new species would be 13.5 mm.

The cephalic shield has a pair of dorso-lateral protuberances near the posterior margins (Pl. 65, fig. 2). Neither the shape of the shield nor the position of the cervical groove is distinctive. Remains of antennae are too poor to warrant comment.

The thorax has eight tergites characterized by transverse grooves. The sixth tergite is the widest and it overlaps both adjacent tergites. Imbrication is as on *P. typus*. The maximum length of the sixth tergite is 1.0 mm, the length of the third is 0.7 mm, and the length of the first is 0.5 mm.

Pleurae of the thoracic somites cannot be seen on the fossil.

Remnants of legs are preserved on the right side of the specimen. The fifth and seventh endopods are long and slender with the joints developed in the manner normal for the genus. Setae can be seen on the carpus and propodus. Mineral fillings of the tubular remains of the epipods are present on the legs of somites three to six (Pl. 65, figs. 1, 2). On the counterpart they can be seen in negative relief on legs two to eight.

The tergites of the first two abdominal somites have the two

characteristic transverse grooves. The pleurae are badly crushed, but their shape can be seen on the compression. It is a pointed lobe. There is a possibility the anterior curvature is not so convex as on *P. typus*.

Copeland (1957 b, p. 47) characterized the caudal fan as follows, "Caudal appendage showing one pair of setate, elongate swimmerettes on either side of the elongate blunted telson plate. Telson with numerous coarse setae ending posterior to the swimmerettes." His figure (1957 b, pl. 15, fig. 1) shows the rami of the uropods poorly preserved. The telson has the typical spatulate shape and is fringed by bristles.

Synopsis.—A new syncarid, *Palaeocaris canadensis*, is described from the Pennsylvanian deposits of Nova Scotia. The species is small in size and characterized by two transverse grooves on each postcephalic tergite.

Stratigraphic occurrence.—The holotype is from the Riversdale group. Specimens figured by Copeland are from the Pictou group. Both are Westphalian, Pennsylvanian.

Localities.—Holotype is from the headland at confluence of Ramshead and Diligent rivers, south of Diligent River, Cumberland Co., N.S., Canada. The specimens previously described are from Clifton and Glace Bay, N.S., Canada.

Collector.—Donald Baird, Princeton University.

Holotype.—The single specimen studied, MCZ 5435, is in the Museum of Comparative Zoology, Harvard University.

Genus **PALAEOSYNCARIS**, new genus

A beautiful fossil syncarid was discovered in a four inch drill core of the Heath shale of Upper Mississippian-Lower Pennsylvanian age from the subsurface of North Dakota. The specimen was obtained from a depth of 8170 to 8180 feet. It missed being damaged by the drill only two sixteenths of an inch. From the counterparts it is possible to determine most of the significant morphological features which prove it to represent a new genus and species.

In many respects, the fossil resembles the specimens described as *Praeanaspides praecursor* by Woodward (1908). Reassignment of

Woodward's species to *Palaeocaris* by Calman (1911 b) must be considered tenuous. The syntypes were large individuals on which the pleurae of the thoracic tergites were short and blunt. All tergites had multiple transverse striae. The new species from North Dakota also has these characteristics but is different in that the posterior margin of the large pleural lobes of the abdominal tergites is coarsely serrate. Whereas the posterior margins of the pleural lobes of Woodward's Pennsylvanian specimens were straight, those of the new genus are rounded. The lateral margins of the exopod of the uropods and the free edge of the telson of the specimen from North Dakota are armed with distinctive small spines, not bristles. Irrespective of the validity of *Praeanaspides*, there is no doubt that a new genus must be established for classification of the new species described below.

***Palaeosyncaris dakotensis*, new species**

Pl. 65, figs. 3, 4; Pl. 66,
figs. 1-3; Text Pl. 14, fig. a

The body of the specimen is 24.5 mm. and the telson is 4 mm. in length. Lengths of the tagmata are as follow: head, 3.5 mm.; thorax, 10.5 mm.; and abdomen (*sans* telson), 11 mm. It is believed the proportional development and the transverse ornament on the tergites are distinctive of this species.

Description of the specimen.—The specimen is preserved as a compression in a black shale. Remnants of the chitinous exoskeleton remain on one of the counterparts. The other is an impression. Associated specimens of *Pseudoestheria* sp., ostracods, and *Anthraconaia*-like pelecypods are partially pyritized. The exoskeleton is oriented such that its left ventral side is bent under. Exposed are the dorsal and right lateral portions of the fossil. Even compensating for the great exaggeration in body depth due to compressional spreading, the animal was considerably more robust than any of the species of *Palaeocaris*.

The head is the most poorly preserved portion of the fossil. Nothing except the length of the head shield can be determined. However, stalked compound eyes and all elements of both antennae are remarkably well displayed. The peduncle of the eye is relatively long and slender. The hemispherical cornea is comparatively small for a syncarid.

The peduncle of the first antenna consists of three joints. The basal joint is equal in length to both of the others (Pl. 66, fig. 2). There are remains of both annulate rami. These flagella are fragmentary, but appear to have been somewhat longer than those of *Palaeocaris*. Sockets for the origin of fine setae are preserved along the distad margin of several of the annuli. This is the only fossil syncarid known to have setigerous flagella. It is a characteristic of the Recent Syncarida.

The second antennae (Pl. 65, fig. 3) have the typical elements. The second joint of the sympod, the major part of which serves as a stipe for the scale, is unusually stout. The antennal scale is small, lobate, and fringed with setae. The flagellum is setiferous and apparently not of great length.

Of the other cephalic appendages only the body and incisor lobe of the mandibles are distinguishable. The body of the mandible is not so large as the mandibles of *Palaeocaris* and *Acanthotelson*.

The thorax consists of eight somites. The tergite of the first is reduced to a narrow band, but it is free and definitely is not fused with the cephalon. The second tergite is narrower than the six subequal thoracic tergites succeeding. From the fossil it is impossible to be certain if there was forward imbrication of the anterior tergites. They appear to all overlap to the posterior. Irregular, transverse striae cross each tergite and terminate upon the pleurae. Typically there are three, but some of the posterior thoracic tergites have four. The pleurae of the anterior tergites are short. The free ventral margin is transverse with the anterior and posterior rounded. The pleural lobes become progressively longer and more oblique. The eighth lobe is pointed.

The thoracic legs are remarkably well preserved except for the epipods and exopods of which no trace remains. The sympod consists of two short joints as can be distinguished on the third, fifth, sixth and seventh appendages. The five joints of the endopod can also be seen on these pereiopods. The legs are much shorter and stouter than those of *Palaeocaris*. Only scraps of the first thoracic endopod are present and reduction in size is indicated. The second appendage is not unlike the typical posterior pereiopods; however, the third seems to be somewhat longer and more heavily constructed.

There was a tendency for the development of large raptorial appendages in the Paleozoic Syncarida, e.g., *Acanthotelson* and *Uronechetes*. Though not distinctly specialized, the third thoracic endopod of *Palaeosyncaris* appears to have been incipiently modified.

The first five abdominal tergites are of subequal length whereas the sixth abdominal tergite is nearly twice as long. The abdominal tergites are characterized by having large pleural lobes and four transverse striae. The ventral margin of each lobe was heavily chitinized and produced as a posterior spine. The free posterior edge of the lobe dorsal to the spine was convexly curved and armed with long pointed teeth (Pl. 66, fig. 3). The sixth abdominal segment lacks pleural lobes. Pleopods are unknown. Only the single jointed sympod and the lobate exopod of the uropods are partially preserved (Pl. 65, fig. 4). Spines on the convex outer margins of the exopod are more abundant and rigid than on any other syncarid.

The telson is spatulate with a broad base. Distinctive rigid spines are borne on the postero-lateral and rounded terminal portion of its margin.

Synopsis.—The new genus, *Palaeosyncaris*, has blunt pleurae on the anterior thoracic tergites. These change posteriorly to the longer pointed pleural lobe of the eighth thoracic somite. Large pleural lobes with a ventro-posterior spine and a convex, serrated posterior margin are distinctive of the first five abdominal somites. Whereas the other Paleozoic syncarids have their uropods and telson armed with setae or bristles, the rigid, pointed processes on this genus are best designated as spines. The pereopods are relatively short and massive. The third pair is somewhat large and may have been incipiently modified as raptorial appendages. The general aspect of the fossil gives the impression of a creature with a more massive body than that of the other syncarids. It is believed the transverse ornament on the tergite is a specific criterion as are the relative proportions of the body.

Stratigraphic occurrence.—Heath shale, Upper Mississippian-Lower Pennsylvanian.

Locality.—Subsurface from core approximately 8170 to 8180 feet in Casimer Duletski No. 1, Tennessee Gas Transmission Company, N.W. 1/4, N.W. 1/4, Sec. 16, T. 139 N., R. 99 W., west southwest of Dickinson, Stark Co., North Dakota.

Holotype.—One counterpart is in the collection of the University of North Dakota, Grand Forks, North Dakota, and the other is in the collection of the U.S. National Museum, No. 143409.

Genus **SQUILLITES** Scott, 1938

The author of this name clearly expressed the intention that the name was proposed to discriminate a distinct genus for a Mississippian crustacean from Montana. The name was selected because it was believed the fossil was closely related to *Squilla*, a Recent stomatopod. Herein, this relationship is disproven.

Squillites is characterized by having 14 free post-cephalic somites. Eight thoracic somites contribute as much to the length of the animal as do the six abdominal somites. There is no carapace. The first thoracic tergite is narrow and overlaps onto the posterior of the head. Most distinctive are the similar sternites of all post-cephalic somites. They are relatively wide with rounded lateral margins. The rami of the uropods are spatulate and fringed with setae. The massive telson is wedge-shaped and armed with stout bristles.

The type species is *S. spinosus* Scott, 1938. The genus is monotypic.

Squillites spinosus Scott, 1938 Pl. 53, figs. 1, 3; Text Pl. 14, fig. d

Squillites spinosus Scott, 1938, p. 508-510, 2 figs.

Squillites spinosus, Berry, 1939, p. 467.

Re-interpretation of the specimen invalidates the original definition. After the morphological analysis, characterization of the species will be summarized in the synopsis. A restoration is impossible but a diagrammatic drawing of the specimen is presented with the parts labeled (Text Pl. 14, fig. d.)

Description of specimen.—This small crustacean is preserved as dorsal and ventral impressions in a black shale matrix. The chitinous exoskeletal compression has disintegrated. Not having previously worked with fossil Malacostraca, it is a tribute to Scott that he distinguished so many morphological features correctly. The specimen is most confusing until one realizes the specimen is twisted. The front portion of the animal presents the right side, whereas the posterior is a left dorso-lateral view. Ventral features have been impressed into the dorsal integument where it is preserved. Except

for the left pleurae of the sixth and seventh thoracic somites, the dorsal skeleton is missing for the third to the seventh. Though dorsal and ventral structures are superimposed, one counterpart (Pl. 53, fig. 1) portrays the dorsal feature best, whereas the other shows the ventral (Pl. 53, fig. 3).

Measurements are as follow: length of body, 7.8 mm.; length of head, 1.1 mm.; length of thorax, 3.3 mm.; and the width of the eighth sternite is 1.1 mm. Widths of other features presented by Scott (1938, p. 510) are of no significance as their great width is due to compressional spreading.

The head shield is poorly preserved. Its length is equal to slightly less than one-seventh the length of the complete body. It appears that the mid-dorsal edge of the carapace projected forward. The extent to which a rostrum was developed is unknown.

A composite of parts exists in front of the cephalic shield. Only the three flagella that extend beyond this complex are interpretable. The two long flagella with large annuli are probably the endopods of the second antennae. Because of equivalency in size of the annuli, it is doubted that the less complete one is the remains of a first antenna as believed by Scott. Vague remains of a minute flagellum exist between the two larger flagella. This is all that is known of the first antenna.

The eight thoracic somites are free and not covered by a carapace. A narrow tergite overlaps the posterior margin of the head. The second thoracic tergite is twice as wide. It also imbricates forward. Tergites three to five are not preserved. The sixth and seventh are represented only by their left pleura. The eighth is complete and the true shape of the pleura is shown. It is bluntly pointed. The postero-lateral angle of this lobe results from a broad curvature of the antero-ventral edge.

All eight thoracic sternites can be distinguished on both counterparts. The first is reduced in size. On the fossil, it is displaced posteriorly and is associated with the second tergite. The lengths of the succeeding thoracic ventral sclerites are longer. A rounding of the lateral margins of these strongly sclerotized plates is a singularity. Foramina for the legs can clearly be seen on the seventh sternite.

A clue to interpretation of the abdomen is found in the remains of the eighth thoracic somite. Both tergal and sternal features are clearly superimposed. Not only are the lateral extremities of the sternite strongly expressed on the fossil, but the right pleura is bent under in such a way that the tergite appears to have three longitudinal ridges. These are the "prominent knobs, one median and two laterals" mentioned by Scott (1938, p. 508-509). No ornament of any type was seen.

The dorsal and ventral skeletal features of the six abdominal somites are as described for the thorax. They are all of subequal length. The sternites narrow posteriorly. Foramina for the appendages are clearly evident on some of the sternites. Except for the large uropods arising from the sixth abdominal somite, no post-cephalic appendages were detected. The basal sympodal joint of the uropods gives rise to two long spatulate rami. Both the exopod and endopod have a median keel. A fringe of setae surrounds the outer as well as the inner margins of the two lobes.

The telson appears to have been a heavy wedge-shaped body. Accessory furcal structures are not present. It is believed the complete free margin was armed with heavy bristles. Evidence for these is found in the large sockets at the edge of the telson.

Synopsis.—Scott recognized that this crustacean lacked a carapace. However, because of spreading of the abdomen, its relatively enormous appearance on the fossil misled him to believe it was a stomatopod. Actually the thorax and the abdomen are about the same length. Using the width of the abdominal sternites as a criterion, the abdomen was of normal width and diminished in size posteriorly.

The true affinity of this crustacean is with the Syncarida. Not only are all eight thoracic somites free, but the tergites of at least the first and second imbricate forward. This is an irrefutable criterion peculiar to the Syncarida in Crustacea. Lack of articulated furcal processes on the telson is of less significance.

The peculiarity of the sternites with their rounded lateral extremities and the massive wedge-shaped telson are generic characteristics. Lack of ornamentation and the proportional development of the various morphological parts will probably prove to be the basis for specific distinction.

Stratigraphic occurrence.—Heath shale, Big Snowy group, Chesterian, Mississippian.

Locality.—Two miles south of Heath, Fergus County, Montana in Spring Creek on the north flank of the Big Snowy Mountains.

Collector.—Harold W. Scott.

Type specimen.—Counterparts of holotype are X-1219 in the University of Illinois collections.

IDENTITY OF AMPHIPELTUS, DIPLOSTYLUS, AND EILETICUS

Three genera of fossil arthropods from North America are in need of restudy; they are *Amphipeltus* Salter, *Diplostylus* Salter, and *Eileticus* Scudder. From evidence now available, I believe the first two are abdomens of *Pygocephalus dubius* (Milne-Edwards), and that *Eileticus* is a myriapod as originally reported, through specimens subsequently assigned to this genus are species of the syncarids, *Acanthotelson* and *Palaeocaris*.

Salter (1863 a, p. 75-78) established *Amphipeltus paradoxus* and *Diplostylus dawsoni* for two fossil crustacean abdomens. The first fossil, which also has the cephalothorax poorly preserved, is allegedly from the Devonian rocks near St. John and the second is from the Coal Measures at Joggins, Nova Scotia. It is mentioned that fragments of a fern and *Cardiocarpon* occur on the same slab of black glossy shale as the holotype of *A. paradoxus*. *Cardiocarpon* is a Pennsylvanian seed. Though Dawson (1862), the collector, claimed the specimen was collected from Devonian strata, the presence of *Cardiocarpon* and the similarity of the abdomen of the figured specimen to that of *Diplostylus dawsoni* (Salter, 1863 a, figs. 6, 11) makes this determination highly improbable. The specimen (having five tergites bearing pleural spines directed backward) which was later figured by Matthews (1895, pl. 2, fig. 6) from the Little River Group of Devonian age, represents a different type of arthropod. It is certainly not an isopod as Matthews claimed. Until proven otherwise, Salter's two genera must be considered as synonyms and they are probably incorrectly interpreted abdomens of

Pygocephalus dubius (Milne-Edwards), a crustacean known to occur in the Pennsylvanian strata of Nova Scotia.

The holotype of *Eileticus anthracinus* Scudder (1882, p. 178-189) is a typical myriapod from the Pennsylvanian concretions from Mazon Creek, Illinois. The unmistakable broad labrum of the Archipolypoda is present on the specimen originally illustrated. By later figuring poor specimens of *Acanthotelson stimpsoni* Meek and Worthen (USNM 38004) as an additional example of *Eileticus anthracinus* and as specimens of a new species, *E. aequalis*, Scudder (1890, p. 420-421, pl. 38, figs. 5-9) (USNM 37996) misled European paleontologists. Pruvost (1919, p. 89) recognized the syncarid nature of these later specimens and thus classified *Eileticus*, *Acanthotelson* and *Pleurocaris* in the family Acanthotelsonidae. Recently Vandenberghe (1960, p. 690-692) synonymized *Pleurocaris* Calman (1911 a, p. 156-160) as a junior synonym of *Eileticus*. The new species he proposed, *E. pruvosti*, from the Saint-Etienne Basin of France is too poorly illustrated for positive determination, but it is probably a species of *Palaeocaris*. It should be noted that his observations, that the first thoracic somites are incorporated into the cephalic tagma and that the abdomen has seven somites, are erroneous. As in *Palaeocaris*, there is the typical eumalacostracan segmentation of the tagmata, *i.e.*, five cephalic, eight thoracic and six abdominal somites. He simply placed the division between the tagmata incorrectly. Adding further to the confusion, a new family, Eileticidae, and a new subfamily, Anacanthotelsonidae, were proposed. He also reduced Acanthotelsonidae Cockerell (incorrectly attributed to Pruvost) to subfamily rank. Not being aware of the incorrectness of the premises upon which Vandenberghe's classification of the Paleozoic Syncarida was based, Rolfe (1962, p. 550) revised the family and subfamily names. The taxonomy of both authors must be rejected, and *Eileticus anthracinus* Scudder remains a valid name for a species of Pennsylvanian myriapod.

STRATIGRAPHIC OCCURRENCE AND PALEOCOLOGY

The stratigraphic occurrence of fossil arthropods with skeletons not fortified with mineral matter is extremely sporadic. Many types

of arthropods have evolved and become extinct without leaving any trace of their existence. The Euphausiacea must have existed throughout Mesozoic and Cenozoic time, but no fossils are known.

For an example of the extent to which ecological factors and selective preservation influence the stratigraphic occurrence of fossil arthropods, and the misconceptions that have resulted, one has only to cite the fossil record of the limuloids (Brooks, 1957, p. 896). Recent *Limulus* and its congeners are marine animals (Waterman, 1953), though in the breeding season they migrate to the beaches. They invade lagoons, estuaries, swamps, and sometimes wander for considerable distances up rivers. Undoubtedly, the Tertiary, as well as the Mesozoic limuloids, had similar habits. It is interesting to note that there is not one occurrence of their remains preserved in typical marine sediments. Remains of limuloids are found in association with trachaeophytes in fresh to brackish water, lagoonal and swamp deposits, and in sediments that contain evidence of supersalinity. The one example in which they occur in a marine deposit is the lagoonal Solnhofen limestone of Bavaria. This is a Jurassic back reef deposit in which marine organisms, including several genera of decapods with chitinous skeletons otherwise unknown as fossils, are associated with terrestrial animals, *i.e.*, insects, arachnids, and vertebrates. Their fossil record is a paradox unless one realizes the stratigraphic occurrence is the result of selective preservation and special environmental conditions under which the remains were preserved. In the sea, the normal habitat, their chitinous exoskeletons were destroyed.

The species of *Archaeocaris* and *Palaeopalaemon* are the only fossil Paleozoic Eumalacostraca with fortified skeletons, and they were originally weakly mineralized. Their remains are found in sideritic and phosphatic concretions in marine deposits. The single specimen not from a concretion, *Archaeocaris graffhami*, was collected from a light tan, calcareous shale associated with abundant goniatites and remains of other marine animals with shells. The Mesozoic and Tertiary lobsters with a larger more heavily fortified chitinous exoskeleton have left a record that is not much better than that of their Paleozoic counterparts (Brooks, 1957, p. 896). Their fossil record consists mostly of the strong chelae, and these are rare.

In the normal marine environment chitin is rapidly destroyed by fungi and bacteria. It is only where biological and physicochemical factors have favored their preservation that the chitinous Paleozoic eumalacostracan remains are found. These are the anaerobic conditions in marine and lagoonal environments wherein biological activity is arrested in organic rich muds. Supersaline and fresh water environments also favored their preservation. The other condition indicated by the fossil record is that of a lagoon which has fluctuated from fresh to salt water conditions.

The oldest eumalacostracan fossils are found in the Devonian and these are uncommon. The known world record is eight specimens. Two species are from the Upper Middle Devonian. They are *Eocaris oervigi* Brooks (1962 a) from the Givetian of Western Germany and *Devonocaris cuylereensis* (Wells) from the Moscow formation of New York. Both are known from single poorly preserved fossils. Directly associated with *Eocaris* in a gray siltstone are fish remains and an archaeostracan, *Montecaris lehmanni* Jux. Typical marine invertebrate fossils also occur in the same formation (Jux, 1960). The Moscow formation in which *Devonocaris* occurs is a black marine shale. Only two additional species of Devonian Eumalacostraca are known. They are *Devonocaris destinezi* (Van Straelen) from a subgraywacke of Belgium and *Palaeopalaemon newberryi* Whitfield from the Upper Devonian black shales of Ohio. The same American species is also known from a phosphatic concretion from the Lower Mississippian of Kentucky.

In Mississippian strata eumalacostracan fossils become more abundant. Most occur as compressions in black carbonaceous shales associated with scraps of plants, fish, and miscellaneous fossils which have led paleontologists to infer a fresh-water habitat. However, the relatively rare species of *Archaeocaris* and *Palaeopalaemon* are found in unquestionably marine deposits. Most of the Mississippian fossils have been collected from Scotland (Peach, 1908). A few are known from France (Carpentier, 1913). Less than 30 specimens have been collected in North America. *Anthracocaris* (Calman, 1932 b) from Scotland and *Acadiocaris* redescribed above from Nova Scotia were originally reported as syncarids (Peach, 1908, Copeland, 1957 a). Both genera have a short carapace and are thus not syncarids.

Syncarids made their first appearance in the uppermost Mississippian of North Dakota and Montana in a black shale. *Palaeosyncaris* is associated with estherians, *Anthraconaia*-like pelecypods and "fresh water ostracods." *Squillites* occurs in a facies of the same formation with more characteristics of being marine.

With both syncarids and pygocephalomorphs occurring in the black shales and ironstone concretions associated with Pennsylvanian coal deposits, eumalacostracan fossils are no longer uncommon. *Anthracaris*, *Pygocephalus*, *Anthracophausia*, *Pseudotealliocaris*, *Belotelson*, *Acanthotelson* and *Palaeocaris* occur in strata of Pennsylvanian age in North America. Though hundreds of some of these animals have been collected, only *Palaeocaris* is represented by more than one American species. This is further evidence of the inadequacy of the paleontological record.

The presence of plant remains, *Anthraconaia*, merostomes, arachnids, insects, myriapods, estherians, and fish, have been deceptive in environmental arguments. A common fossil in all of these deposits is *Spirorbis*, a sedentary, tubicolous, marine polychaete. Other marine fossils also occur but tend to be overlooked by those who have a preconceived interpretation. Mazon Creek concretions contain excellent specimens of marine gastropods, amphineurans and pectenoid clams. One trilobite has been collected (Richardson, 1956, p. 59). The deposit is at the margin of the Pennsylvanian marine embayment into northern Illinois.

In the infancy of geology, plant remains and estherians were used as criteria for fresh-water conditions of deposition of Upper Paleozoic strata. The occasional presence of insects, arachnids, myriapods, and amphibian remains gave further weight to the argument. However, one has only to cite the occurrence of terrestrial animals in the Jurassic Solnhofen limestone to demonstrate the need for caution. Actually a complete re-evaluation is needed of the habitat and conditions of preservation of all the alleged "fresh water faunas" from Paleozoic rocks. The only reliable evidence will be obtained by geochemical studies. Could it be that the Upper Paleozoic estherians were marine or at least euryhaline? It is known that the Devonian species were marine (Raymond, 1946).

If one were blindly to accept the criteria presently used as evi-

dence, we could only conclude that aquatic arthropods with chitinous exoskeletons colonized the fresh-water environment during the Carboniferous and were restricted to it in the Permian. It is my opinion that the Mazon Creek fossiliferous deposit is lagoonal in origin. Its salinity may have fluctuated and the lagoon may have been fresh for short periods of time. It is also possible that the Crustacea were euryhaline and tolerated the freshened conditions. That they were not marine organisms cannot be upheld merely because of "scientific" tradition. The absence of their skeletal remains in normal fossiliferous marine deposits is negative evidence caused by selective preservation. It is absurd to perpetuate as fact, paleoecological interpretations based upon circular reasoning and negative evidence.

Some of the Permian syncarids and pygocephalomorphs may have lived in fresh water as their normal habitat, but this is improbable. The deposits in which the single Permian specimen from Texas occurs (Wilson, 1953) may be fresh water in origin, but the specimens of the same species, *Mamayocaris jepsemi*, from the Opeche formation of South Dakota were collected from a lagoonal deposit. Beurlen has called attention to the fact that the syncarids and pygocephalomorphs from the Permian of Brazil are found associated with a marine fauna (1931, p. 46-49). It is obvious that he would like to believe they were fresh-water animals so he concludes the environment was "at least not completely marine".

A criterion for interpreting the feeding habits of the most ancient Eumalacostraca is found in the fossils of the Pennsylvanian syncarids, *Acanthotelson* and *Palaeocaris*, which lived in the same habitat and were similarly preserved. *Acanthotelson* was primarily a rapacious carnivore as indicated by the modification of its anterior thoracic legs. The fossils of the more generalized *Palaeocaris typus* have detrital fillings of the intestinal tract whereas, with one exception, those of the associated carnivore do not. The size frequency distribution of the individuals in the statistical sample of the two species may also be of ecological significance (Text Pl. 12, figs. b, c). The population of *Acanthotelson* is skewed with some individuals attaining sizes twice that of the mode, whereas *Palaeocaris* has a size distribution with the mode skewed toward the larger sizes typical of paleontological samples of scavengers, microphagous feeders and herbivores. The population of *Acanthotelson* has its modern cor-

relation in the Recent carnivorous lobsters. In Recent slime- and detritus-feeding crustaceans large amounts of sediment are taken in with the food. Thus, one can only conclude that *Palaecaris* fed on bottom detritus. If this criterion can be extended to the other Paleozoic fossils, then *Devonocaris*, *Teallicaris*, *Anthracaris* and most of the other eumalacostracans were bottom scavengers. As further evidence in support of the argument, fossils of *Archaeocaris* and *Perimecturus*, the rapacious stomatopod-like Paleozoic crustaceans are the other exceptions to having casts of the intestinal tract. With their subchelate raptorial appendages, large abdomens, and short carapaces these creatures, by Dollo's (1910) principle of form and function, are believed to have been carnivores and to have had burrowing habits such as do the Recent stomatopods.

Evidence for the feeding habits of the Paleozoic Eumalacostraca is inconclusive, but it is a mistake to accept dogmatically the postulate that the ancestral Eumalacostraca were filter feeders (Cannon and Manton, 1927; Dennel, 1937). Notwithstanding the nauplius type "primitive" mandibles of the Mystacocarida, which may represent an example of phylogenetic neoteny, the typical crustacean jaw is a biting triturating structure. If filter feeding is the primitive mode of obtaining food, the evolution of the crustacean mandible is a singular exception to Darwinian theory. From the multiplicity of filtering methods that exist in the Crustacea (Dahl, 1956), it is safe to assume that filter feeding is a secondarily acquired adaptation. The evidence presented above indicates that primitive crustaceans, and thus the archaeotype of the Malacostraca, were bottom living omnivorous scavengers that fed predominately on detritus.

The shrimplike bodies of *Eocaris*, *Devonocaris*, *Anthracophausia*, *Palaepalaemon*, and *Belotelson* are the only exceptions in the Paleozoic Eumalacostraca of North America to being adapted as predominantly bottom living creatures. The large abdomen relative to the length of the cephalothorax in this caridoid type of crustacean is indicative of nektonic habits. Another analogy of interest is the crablike pygocephalomorphs from the Southern Hemisphere. These benthonic homeomorphs have the abdomen reduced and flexed under the body.

The stratigraphic occurrence of the fossils from North America

are summarized diagrammatically in Text Plate 15. The teilzones of the American Eumalacostraca are plotted in relation to the known biozones of the genera.

PHYLOGENETIC RELATIONSHIPS AND THE CLASSIFICATION OF THE PALEOZOIC EUMALACOSTRACA

In the older papers on fossil eumalacostracans from the Paleozoic, most authors classified the species with a carapace as decapods. The single exception was Huxley (1857, p. 368), who recognized some of the homologies between *Pygocephalus* and the Mysidacea but even he later (1877) referred to its synonym, *Anthrapalaemon*, as a "Macrourous Decapod Crustacean". Woodward (1907 b) figured and described a peracarid marsupium composed of oostegites on *Pygocephalus*. In the following year Peach (1908) published his monographic study on the Upper Paleozoic Eumalacostraca from Scotland in which oostegites also were proven to exist on *Tealliocaris*. He envisioned that a marsupium was present on all other contemporaneous genera. In his text, Peach repeatedly compared the morphological features of *Tealliocaris* with those of the Recent Lophogastridae. Phylogenetic theory at the time advocated the primitiveness of the Lophogastridae and Peach enthusiastically believed the paleontological record supported the theory.

Peach (1908, p. 6) classified the syncarids as "Anaspidae", *Perimecturus* in a new family Perimecturidae, and *Tealliocaris*, *Pseudogalatea*, *Anthrapalaemon* and *Pygocephalus* as Lophogastridae in the "Mysid Group" and *Anthracophausia* and *Crangopsis* in the family Euphausiidae of the "Euphausid Group" of the Schizopoda.

Though subsequent authors have correctly separated the Syncardia, the mysidacean classification for the other fossils has been perpetuated and extended to include *Crangopsis* and *Anthracophausia* (Van Straelen, 1931, p. 23-36; Piveteau, 1953, p. 318). The reason for classification of these genera with the peracarid order was the marsupium on *Crangopsis* figured by Peach (1908, pl. 11). Until recently, little attention has been given to the order

Pygocephalomorpha established by Beurlen (1930, p. 452, 1931, p. 44-46) to distinguish those Paleozoic fossils with a carapace. He mentions *Palaeopalaemon*, *Anthrapalaemon*, *Pygocephalus*, and *Paulocaris* without giving an adequate definition of the new taxon.

The classification of the Recent Eumalacostraca has remained essentially unmodified for over 50 years. This is a tribute to Calman's (1904) understanding of the systematic relationships of these Crustacea. Four divisions, *i.e.*, superorders, are recognized. They are the Syncarida, Peracarida, Eucarida, and Hoplocarida. Recently Siewing (1957, p. 268) proposed an additional taxon, the superorder Pancarida, for the Thermosbaenacea represented by two unique genera discovered subsequent to Calman's work.

The Paleozoic eumalacostracan fossils with a carapace described in this paper have a puzzling combination of morphological characteristics not consistent with the definition of any one of the Recent superorders. They are unique in that all have biramous thoracic appendages with a single joint in the sympod and furcal lobes and a median spine on the telson; however, structural trends toward all the basic eumalacostracan types are displayed. *Tealliocaris* with a brood pouch, no seminal receptacle and with sternal processes may be related to the stock from which the Mysidacea arose. On the other hand, *Anthracaris* lacks oostegites, has a seminal receptacle on the last thoracic sternite of females, and has a secondary articulation between the mandible and the epistome. These are characteristics of decapods! The problems in classification are best exemplified by *Pygocephalus* which not only has a peracarid marsupium, but the seminal receptacle diagnostic of syncarids and decapods. All of these Paleozoic genera have the carapace extended laterally, and it is apparent they belong to one phyletic group. These and the genera *Pseudotealliocaris*, *Pseudogalathea*, *Mamayocaris*, *Notocaris*, and *Paulocaris* are herein considered to represent the order Pygocephalomorpha (Beurlen, 1930, emended). They have the cephalothorax and abdomen of subequal length, or the abdomen is reduced. They were the Paleozoic benthonic eumalacostracans.

The nektonic caridoid facies with a shortened cephalothorax is represented in the Paleozoic by *Eocaris*, *Devonocaris*, *Palaeopalaemon*, *Crangopsis*, and *Anthracophausia*. *Palaeopalaemon* is distin-

guished by the thorax being only slightly reduced in length. It is also of phylogenetic significance for another reason. There is an incipient branchiostegal development of the pleurae of the carapace, and it may have been from such a morphological type that the Pygocephalomorpha evolved. *Eocaris*, *Devonocaris*, and *Palaeopalaeomon* have in common unusually large first antennal sympods. In this study oostegites have not been seen on any of these genera, but Peach (1908, p. 74) claimed they were present on *Crangopis*. This needs reinvestigation. Absolute criteria that prevent the above genera from being classified as Euphausiacea are the single joint of the thoracic sympod and the carapace not being fused with the thoracic somites. The order Eocaridacea is proposed for their classification. Recent euphausiids have retained the primitive telson and are probably specialized pelagic descendants of this primitive eumalacostracan order.

Even more astonishing than the phylogenetic trends indicated above is the evolutionary significance of *Archaeocaris* and *Perimecturus*. They are either remarkable homeomorphs of stomatopods or are their ancestors. These fossils have a short cephalothorax covered by a shallow carapace that is fused with four anterior thoracic tergites and the rostrum is articulated at its base. The abdomen is enormously developed and it is known that the thoracic appendages two to five on *Archaeocaris* are subchelate. Whereas the three posterior subchelate appendages of the true stomatopods are reduced, all four are subequally developed on the Paleozoic fossils, therefore the order Palaeostomatopoda is proposed for their classification.

Fossils representing the Syncarida were known prior to the discovery of extant species. The Syncarida was originally defined by Packard (1885 a) to include only the Pennsylvanian fossil, *Acanthotelson stimpsoni* from Illinois. At the time of Meek and Worthen's last description (1868 b) and Packard's revision the most closely analogous extant crustaceans without a carapace were the Isopoda and Amphipoda. The principal diagnostic characteristics of *Acanthotelson* and thus the Syncarida, as presented by Packard, were the absence of a carapace and loss of the first thoracic tergite through fusion. Though reduced, the first tergite is present as it is on all other Paleozoic syncarids from the Northern Hemisphere.

With the discovery of the Recent "Tasmanian mountain shrimp", *Anaspides tasmaniae* (Thomson, 1893), Calman (1896) established the Syncarida as an order. These extant crustaceans with biramous thoracic appendages and no carapace have the first thoracic somite incorporated into the head, and the females do not have a marsupium. The taxon was extended by Calman to include other fossils, such as *Palaeocaris*, which were known to have the first thoracic somite freely articulated. Subsequently several Recent genera have been discovered. In his later classification of these Crustacea, Calman (1904, p. 159) raised the Syncarida to division rank, *i.e.*, superorder.

The attempts that have been made to establish a systematic classification of the fossil syncarids have been unsuccessful (Chapuis, 1915; Cockerell, 1916; Siewing, 1959; Vandenberghe, 1960; Rolfe, 1962) because of misinterpretation and lack of morphological information. Now that it is known that all the Paleozoic syncarids from the Northern Hemisphere have eight free thoracic somites as do the aberrant extant subterranean Bathynellacea, a workable classification is possible. The Bathynellacea have the telson and last abdominal somite fused together, a furca is present, and the pleopods are reduced or absent. Thus they differ from the Paleozoic syncarids from the Northern Hemisphere. In a separate paper dealing with the two authentic anaspidacean fossils known, *Clarkecaris* (Mez-zalira, 1952) from the Permian of Brazil and *Anaspidites* (Brooks, 1962 b) from the Triassic of Australia, I have revised the families and orders of the Syncarida. A new order, Palaeocaridacea, was established for the Paleozoic syncarids that have eight free thoracic somites and the telson devoid of a furca (Brooks, 1962 b). Though the ocellus has not been detected, it may have been present on one or more species of the genera included in this taxon. Primitive characteristics discovered that are not present on extant species of the orders Bathynellacea and Anaspidacea are ocular papillae on the eye stalks of *Palaeocaris typus* and nephropores for antennal glands on the basal joint of the second antennae of *Acanthotelson stimpsoni*.

Evolution of the three orders of syncarids has been discussed separately (Brooks, 1962 b). The most primitive syncarids known are the extant Bathynellacea which have eight separate thoracic

somites, no seminal receptacle on the females, and a furca on the telson. The Palaeocaridacea differentiated and thrived during the Upper Paleozoic. From the Palaeocaridacea, the Anaspidacea evolved in the Southern Hemisphere during the Permian. On *Clarkecaris* from Brazil a vestige of the first thoracic somite can be seen though it is incorporated into the head, whereas on the Triassic fossil from Australia, *Anaspidites*, it has lost its identity within the cephalic tagma as is the condition in the Recent *Anaspides*, *Paranaspides*, *Koonunga*, and *Micraspides*.

Until more is known of the morphology of *Anthracocaris* (Calman, 1932 b) and *Acadiocaris*, n.g., which have a short carapace, we must accept the suggestion of Calman that they are related to the Peracarida. They could be ancestral tanaidaceans as mentioned or related to the Spelaeogriphacea. Both of these peracarid orders have a short carapace covering only the anterior thoracic somites. There are only two unique diagnostic characteristics of the peracarids. These are a lacinia mobilis on the mandible and a marsupium formed of oostegites on the females. It is only the oostegites that we may expect to find preserved on the fossils. If they are present, a peracarid relationship would be proven. The fossils cannot be considered true tanaidaceans even if oostegites prove to be present since these peracarids have the telson fused with the last abdominal somite. Members of the Superorder Pancarida, i.e., *Thermosbaena* and *Monodella* of the order Thermosbaenacea, also have a short carapace and must not be neglected in an analysis of the phylogenetic relationships of the fossils. In the females of the Pancarida the carapace functions as a dorsal marsupium. Also, it is a remote possibility that *Anthracocaris* and *Acadiocaris* are an ancestral stage in the evolution of the Syncarida, or they may not be closely related to any extant taxon. A new order, Anthracocaridacea, is definitely justified by the known morphological features of the fossils, but proof of its relationships with the Peracarida, Pancarida, and the Syncarida must await further discovery. The order Anthracocaridacea is tentatively assigned to the Peracarida.

Several genera of inadequately known Paleozoic arthropods have been referred to the isopods. Because of the previous misinterpretation of *Acanthotelson*, it has been postulated that a rela-

tionship exists between the Syncarida and the Isopoda (Nicholls, 1929, Calman, 1934, Glaessner, 1957 a). This interpretation is not supported by comparative morphology nor the fossils when they are correctly interpreted.

Necrogammarus salweyi Woodward (1871 b) from the Silurian of England, *Praearcturus gigas* Woodward (1871 a) from the Devonian of England, "*Amphipeltus paradoxus*" of Matthews (1895) from the Devonian of Nova Scotia, *Oxyuropoda ligioides* Carpenter and Swain (1908) from the Devonian of Ireland, and *Camptophyllia ethringhami* and *C. fallax* Gill (1924) from the Pennsylvanian of England have been interpreted as isopods. Van Straelen (1931, p. 86) was correct in removing them from serious consideration as representative of any of the Malacostraca. They may be related to the Arthropleurida, an order of Trilobitomorpha. The interpretation of *Palaeocrangon problematicus* (Schlothheim) from the Permian of Germany and England as an isopod has recently been revived by Glaessner (1957 b). Superficial resemblances between these fossils and the phreatoicoids may be misleading. Proof of phylogenetic relationship is lacking on these poorly known fossils.

The Permo-Triassic time was a critical interval in the evolution of the modern eumalacostracan types, but except for the syncarids, fossils are rare in these deposits. *Schimperella beneckeii* and *S. kessleri* Bill (1914, p. 310-322) from the Triassic of France are the oldest authentic mysidaceans. Antiquity of the Mysidacea will be extended to the Pennsylvanian if *Anthracomysis rostrata* Van Straelen (1922, p. M39-M40) from Belgium proves to belong to this taxon. Several genera of primitive decapods occur in Triassic strata. They represent the primitive extant families Peneidae and Eryonidae as well as two extinct families, the Glypheidae and the Pemphicidae. Rapid differentiation of modern decapod types occurred in the Jurassic. Though *Anthracaris* from the Pennsylvanian has some characteristics of the eryonid decapods, it is a pygocephalomorph. The only Paleozoic fossil that may be a true decapod is *Palaeopemphix sosiensis* Gemmellaro (1892, p. 19-20) and related species from the Permian of Sicily. The carapaces figured by Gemmellaro (pl. 4, figs. 1-9) have cervical, post-cervical, and branchiocardiac sulci comparable

to those of *Pseudoglyphea spinosus* and *Pseudopemphix alberti* (Glaessner, 1960, p. 41, fig. 19) from the Triassic. Two species of true isopods have been reported from the Triassic of Europe (Van Straelen, 1931, p. 42, 47). They are *Anhelkocephalon handlirschi* Bill and *Isopodites triasinus* (Picard). Several genera are represented in the Jurassic. The survey of Triassic Eumalacostraca is completed with mention of *Anaspidites* (Brooks, 1962 b) from Australia. It is a true anaspidacean syncarid.

Siewing (1956) has made a detailed study of the comparative anatomy of the extant eumalacostracan types. A wealth of information is employed in the consideration of their interrelationships and his interpretation of the phylogenetic relationship is not likely to be challenged. Both the Syncarida and Hoplocarida are believed to have evolved early in the phylogenetic differentiation of the Eumalacostraca. This conclusion is supported by the fossil record. There is definitely no relationship between the syncarids and isopods. The only evidence for interpretation of the interrelationships and evolution of the Peracarida is comparative anatomy of the Recent species. Siewing's interpretations of the Recent orders of Eumalacostraca are herein accepted but placed in relation to the fourth dimension and the paleontological record (Text Pl. 16). It should be noted that the Decapoda may be polyphyletic. The Penaeidae may have evolved from the Eocaridacea whereas the Eryonidae probably evolved from the Pygocephalomorph. It is likely that the actual ancestral stock for the majority of the decapod types is unknown.

By establishing a new order of syncarids, the Palaeocaridacea, it is possible to logically classify the Paleozoic syncarids. The problem of classification of the Paleozoic Eumalacostraca with a carapace is more difficult. As has been demonstrated, a vertical (phylogenetic) classification for these animals consistent with the taxa established for Recent Crustacea is impossible. Divergent evolution toward modern morphological types can be distinguished, but there is no proof that the Paleozoic species are truly ancestral. Some may be homeomorphs as a result of convergent or parallel evolution. Some of the fossils are too inadequately known for a strict phylogenetic classification and some represent extinct divergent stocks, but most significantly, their inclusion in modern taxa would require

revision and redefinition of established taxonomic units. A vertical classification would be detrimental in that it would obscure the tenuousness of the inferred phylogenetic relationships. It is believed a horizontal classification is the only possible systematic solution. Thus, a new superorder, the Eocarida, is proposed for the extinct orders Eocaridacea, Pygocephalomorpha, and Palaeostomatopoda which have a carapace that is not fused with the thorax, biramous thoracic appendages with a single joint in the sympod, and with furcal lobes and a median spine on the telson. The females may or may not have a marsupium and a seminal receptacle or they may have both.

The resulting classification of the Paleozoic fossils, in which new orders and families are diagnosed is:

Class **CRUSTACEA** Pennant, 1777

Subclass **MALACOSTRACA** Latreille, 1802

Series **EUMALACOSTRACA** Grobben, 1892

Superorder **EOCARIDA**, new superorder

Order **EOCARIDACEA**, new order

Length of thorax reduced, caridoid facies.

Family **EOCARIDIDAE**, new family

Large peduncle of first antennae, no carinae or doublure on carapace.

Genus **EOCARIS** Brooks, 1962

Genus **DEVONOCARIS** Brooks, 1962 (Incertae sedis)

Family **PALAEOPALAEEMONIDAE**, new family

Peduncle of first antennae large, carinae and an incipient branchiostegal keel on carapace.

Genus **PALAEOPALAEEMON** Whitfield, 1880

Family **ANTHRACOPHAUSIIDAE**, new family

Proximal joint of peduncle of first antennae has hollowed out "eye sockets", no carinae or branchiostegal keels on carapace.

Genus **ANTHRACOPHAUSIA** Peach, 1908

Genus **CRANGOPSIS** Salter, 1863

Genus **BELOTELSON** Packard, 1886 (Incertae sedis)

Genus **PALAEEMYSIS** Peach, 1908 (Incertae sedis)

Genus **ANTHRACOMYSIS** Van Straelen, 1922 (Incertae sedis)

Order **PALAEOSTOMATOPODA**, new order

Carapace shallow with articulated rostrum, four posterior thoracic somites freely articulated, thoracic somites two to five subchelate and subequal in size.

Family **PERIMECTURIDAE** Peach, 1908

With characteristics of the order.

Genus **PERIMECTURUS** Peach, 1908

Genus **ARCHAEOCARIS** Meek, 1872

Order **PYGOCEPHALOMORPHA** (Beurlen, emended), 1930

Branchiostegal development of the pleurae of the carapace, cephalothorax and abdomen equal in length, or the abdomen is reduced.

Family **PYGOCEPHALIDAE**, new family

Carapace with antero-lateral spines.

Genus **PYGOCEPHALUS** Huxley, 1857

Genus **ANTHRACARIS**, new genus

Genus **MAMAYOCARIS**, new genus

Genus **PSEUDOTEALLIOCARIS**, new genus

Family **TEALLIOCARIDIDAE**, new family

Carapace without antero-lateral spines, and thoracic sternites with sternal processes.

Genus **TEALLIOCARIS** Peach, 1908

Genus **PSEUDOGALATHEA** Peach, 1882 (Incertae sedis)

Family **NOTOCARIDIDAE**, new family

Abdomen reduced and reflexed under thorax.

Genus **NOTOCARIS** Broom, 1931

Genus **PAULOCARIS** Clarke, 1920

Superorder **PERACARIDA** Calman, 1904

Order **ANTHRACOCARIDACEA**, new order (Incertae sedis)

Carapace covering only first two thoracic somites, articulation between sixth abdominal somite and telson not fused.

Family **ANTHRACOCARIDIDAE**, new family

With characteristics of the order.

Genus **ANTHRACOCARIS** Calman, 1932

Genus **ACADIOCARIS**, new genus

Superorder **SYNCARIDA** (Packard), 1885

Order **PALAEOCARIDACEA** Brooks, 1962

Eight free thoracic somites, stalked compound eyes, normal pleopods and no caudal furca.

Family **PALAEOCARIDIDAE** (Siewing), 1959

None of the thoracic endopods modified as raptorial appendages, rami of uropods lobate and telson spatulate.

Genus **PALAEOCARIS** Meek and Worthen, 1865

Synonyms: *Nectotelson* Brocchi, 1880; *Palaeorchestia* Zittle, 1882; *Gasocaris* Fritsch, 1901.

Genus **SQUILLITES** Scott, 1938

Genus **PALAEOSYNCARIS**, new genus

Family **URONECTIDAE** Cockerell, 1916

Endopods of second thoracic appendages raptorial, rami of uropods lobate and telson spatulate.

Genus **URONECTES** Bronn, 1850

Family **ACANTHOTELSONIDAE**, Cockerell, 1916

Second and third thoracic appendages raptorial, rami of uropods and the telson styloid.

Genus **ACANTHOTELSON** Meek and Worthen, 1865

Family **PLEUROCARIDIDAE** (Chappuis), 1915

None of the thoracic appendages specialized for raptorial purposes, large thoracic pleurae, rami of uropods and the telson styloid.

Genus **PLEUROCARI** Calman, 1911

Order **ANASPIDACEA** (Calman), 1904

First thoracic somite incorporated into cephalic tagma, seminal receptacle, no furca.

Family **ANASPIDIDAE** Thomson, 1894

Exopods on thoracic appendages one to seven, endopods of pleopods reduced, stalked compound eyes.

Genus **ANASPIDITES** Brooks, 1962

Family **KOONUNGIDAE** Sayce, 1908

No scale on second antennae, eyes sessile, last two thoracic limbs are uniramous and the pleopods are all uniramous, except the first two in males which are copulatory organs. No fossils known.

Family **CLARKECARIDIDAE** Brooks, 1962

Vestige of suture between head and first thoracic somite, sigmoidal anterior sulcus on cephalon, long spinelike abdominal pleurae.

Genus **CLARKECARIS** Mezzalira, 1952

Order **BATHYNELLACEA** (Chappuis), 1915

Eight free thoracic somites, telson fused with sixth abdominal somite, furca, pleopods reduced or absent, no seminal receptacle.

Family **BATHYNELLIDAE** Chappuis, 1915

No fossils known.

Superorder **EUCARIDA** Calman, 1904

Order **DECAPODA** Latreille, 1802

Family **GLYPHEIDAE** Winckler, 1883

Genus **PALAEOPEMPHIX** Gemmellaro, 1892

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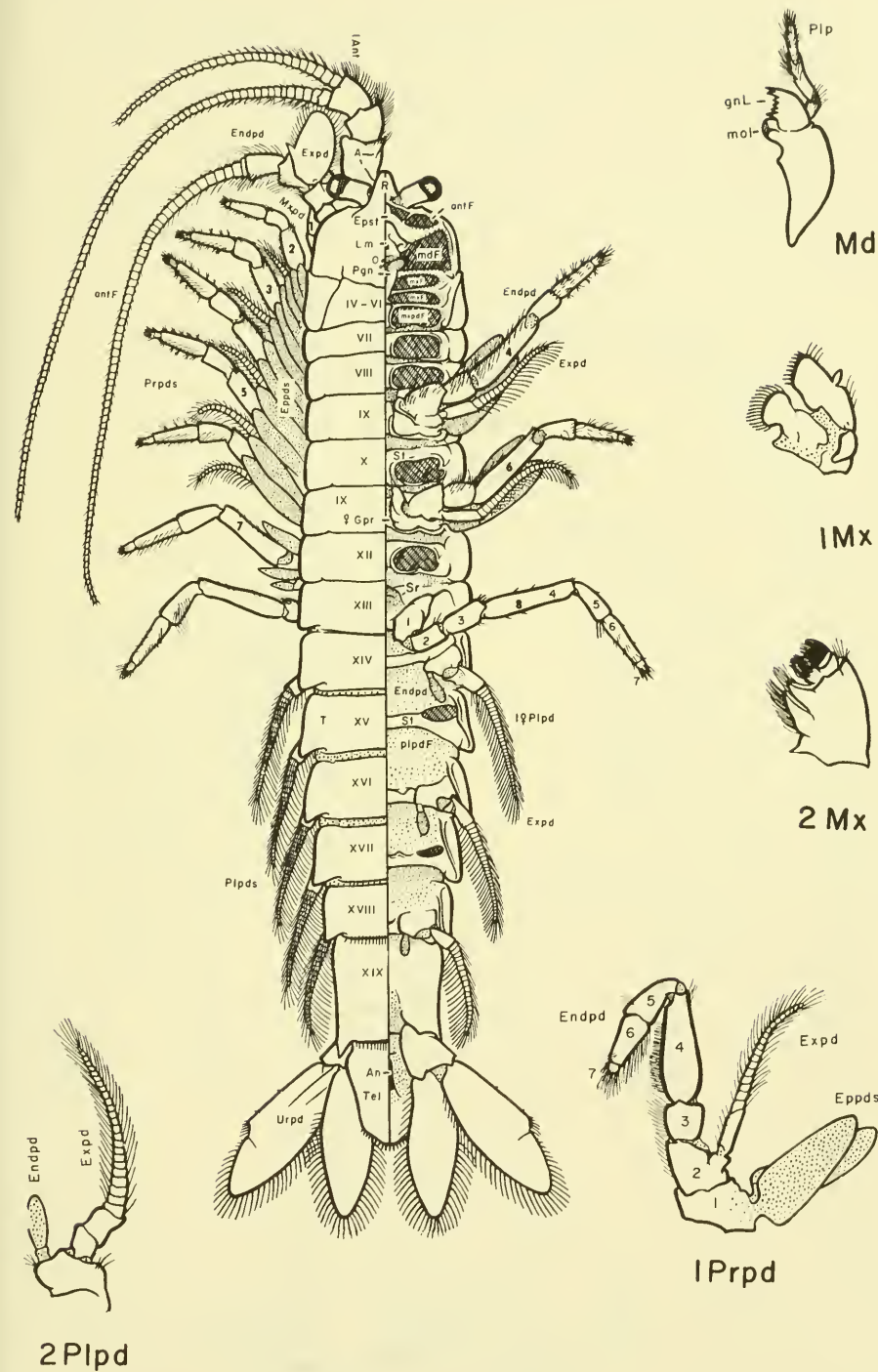
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PLATES

Explanation of Text Plate 1

| | Page |
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| Anaspides tasmaniae (Thomson) | 170 |
| Dorsal and ventral skeletal morphology of the left side diagrammatically drawn; X 5. Representative appendages have greater enlargement. | |



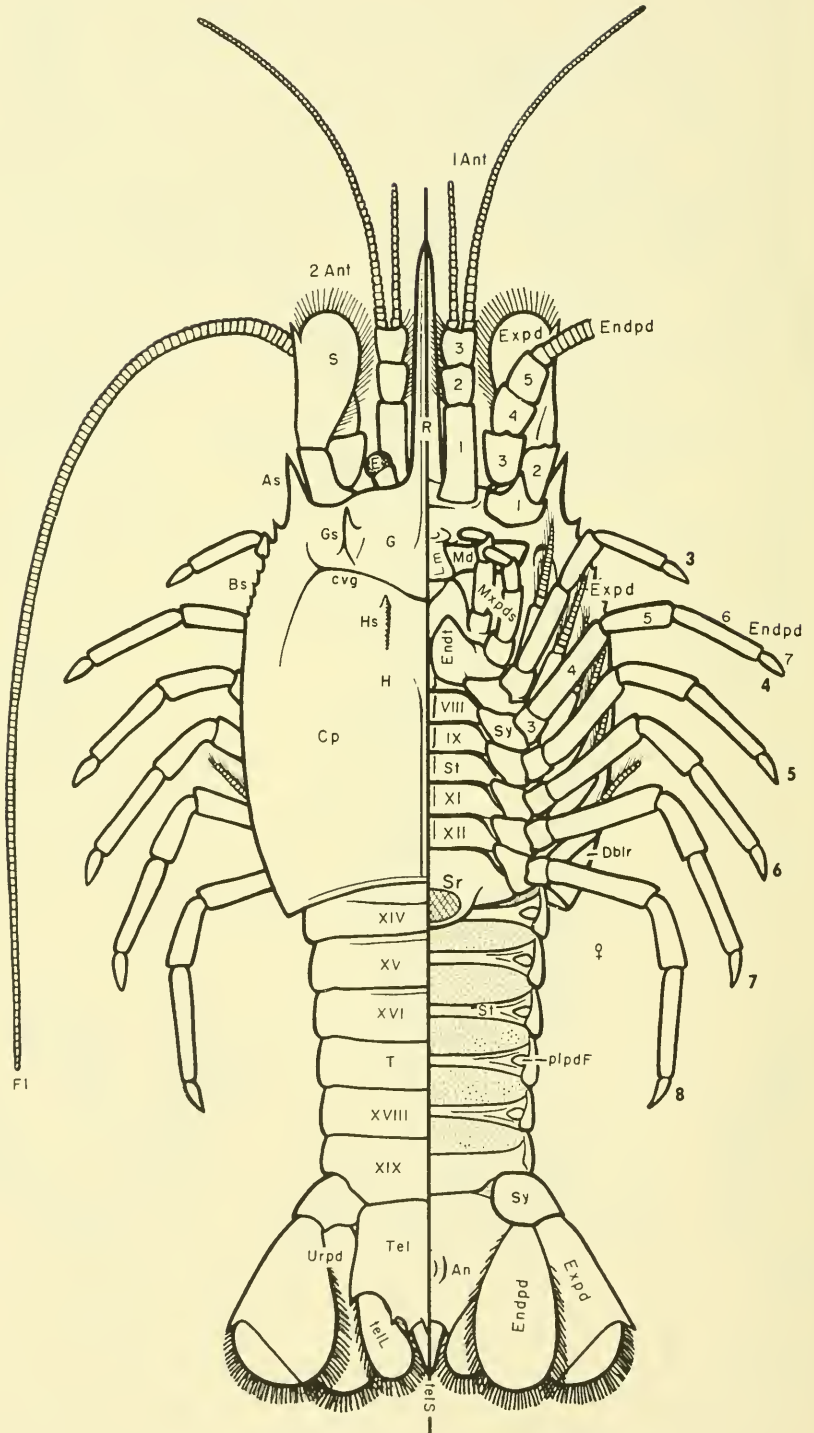
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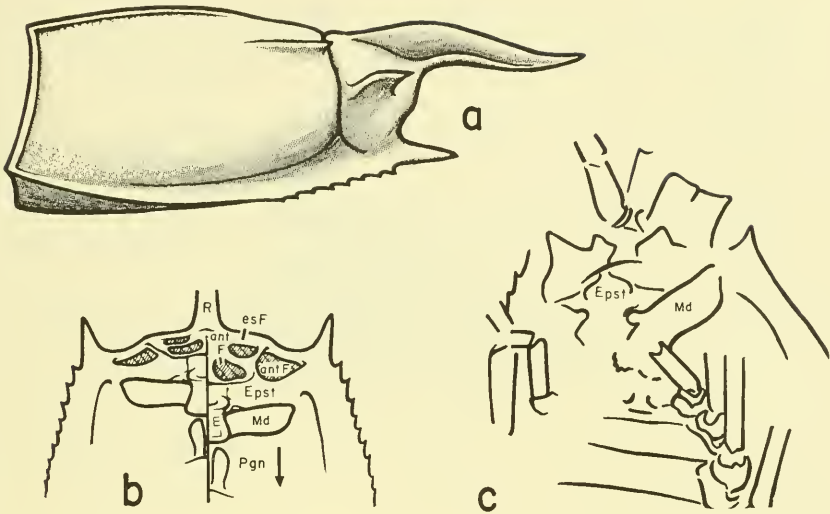


Explanation of Text Plate 2

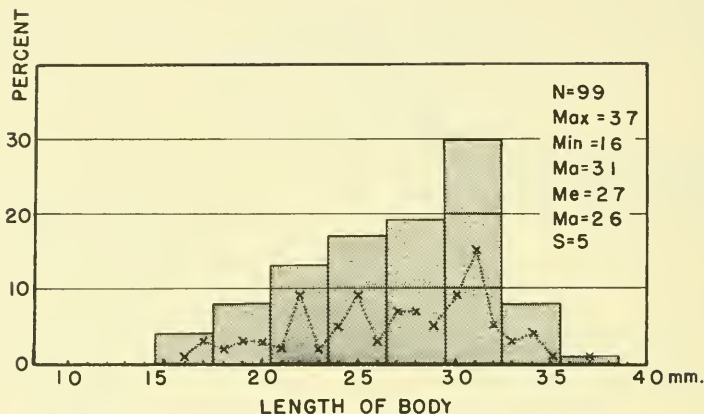
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| Anthracaris gracilis (Meek and Worthen) | 173 |
| Dorsal and ventral skeletal morphology of the left side diagram- matically drawn; X 3.5. | |

Explanation of Text Plate 3

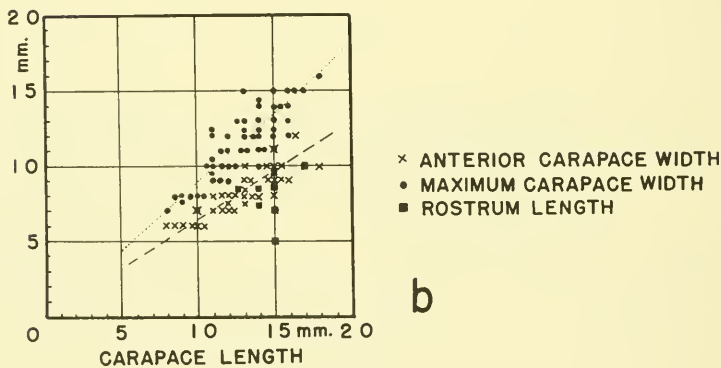
| Figure | Page |
|--|------|
| a. Anthracaris gracilis (Meek and Worthen) Restoration of carapace; X 3.5. | 173 |
| b. A. gracilis Ventral skeletal features of the anterior portion of the head; X 4.5. The right side has been displaced posteriorly to show the shape and position of the foramina. | 173 |
| c. A. gracilis Diagrammatic drawing of ventral skeletal features of PY 19931; note the secondary articulation between the mandible and the epistome. | 173 |
| d. Table of measurements in millimeters of representative specimens of <i>A. gracilis</i> and their proportions. The results of statistical analysis of observations of the total sample are shown at the right. | |



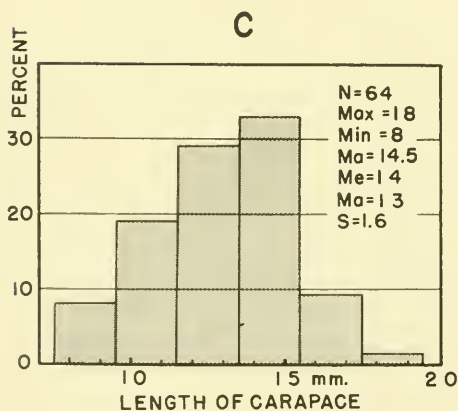
| d | REPRESENTATIVE SPECIMENS | | | | | | | | | | STATISTICAL ANALYSIS | | | | | | |
|--|--------------------------|-------------|---------------|---------|---------|---------|---------|---------|---------|---------|----------------------|-----|-----|-----|-----|-----|-----|
| | ISMNH 3067 | UI X-343 | USNM 38843 | PY19932 | PY19933 | PY19936 | PY19937 | PY19983 | PY19993 | PY19996 | N | Max | Min | Mo | Me | Ma | S |
| LENGTH OF BODY | 24 | 32 | 22 | 26 | 33 | | 37 | 17 | 31 | 31 | 99 | 37 | 11 | 31 | 27 | 26 | 5 |
| LENGTH OF CARAPACE | 12 | 16 | 12 | 11 | 15 | 18 | 15 | 8 | 14 | 13 | 64 | 18 | 8 | 14 | 14 | 13 | 16 |
| CERVICAL GROOVE | | | | 7 | 11 | 13 | 10 | 6 | 10 | 10 | | | | | | | |
| LENGTH OF ROSTRUM | | | | | | | 10 | | 8 | 8 | | | | | | | |
| CARAPACE MAX. WID. | 11 | 14 | 10 | 9 | 12 | 16 | | 7 | 12 | 13 | | | | | | | |
| CARAPACE ANT. WID. | 8 | 12 | 7 | 6 | 9 | 10 | | 6 | | 10 | | | | | | | |
| CARAPACE POST. WID. | 9 | 12 | 8 | 7 | 9 | 10 | | | | 9 | 10 | | | | | | |
| LENGTH OF A-L. SPINE | 1 | 1 | 1 | 1.3 | 1.5 | 2 | | 0.7 | | | | | | | | | |
| SERRATIONS | 5 | 6 | 5 | 8 | 7 | | | 8 | | 8 | 35 | 11 | 5 | 7 | 8 | 8 | 2 |
| PROPORTIONS | | | | | | | | | | | | | | | | | |
| CARAPACE LENGTH: BODY LENGTH | .50 | .51 | .55 | .43 | .45 | | .41 | .48 | .44 | .42 | .45 | .52 | .39 | .50 | .46 | .46 | .04 |
| CARAPACE MAX. WID.: CARAPACE LENGTH | .92 | .85 | .83 | .82 | .78 | .90 | | .88 | .89 | 1.0 | .51 | 1.1 | .68 | 1.0 | .92 | .90 | .10 |
| CERVICAL GROOVE: CARAPACE LENGTH | | | | .64 | .74 | .73 | .73 | .76 | .78 | .77 | .32 | .84 | .64 | .74 | .75 | .75 | .04 |
| ROSTRUM LENGTH: CARAPACE LENGTH | | | | | | | .57 | .59 | .58 | 8 | .80 | .35 | .60 | .60 | .60 | | |



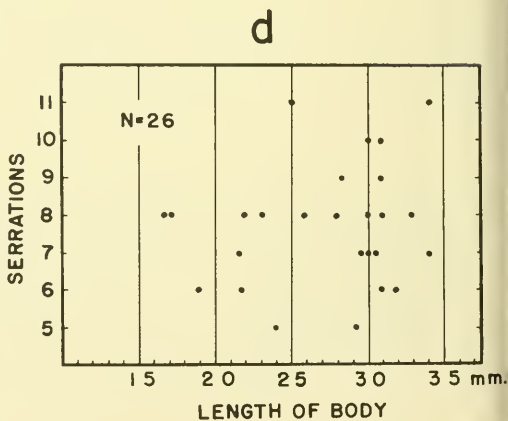
a



b



c



d

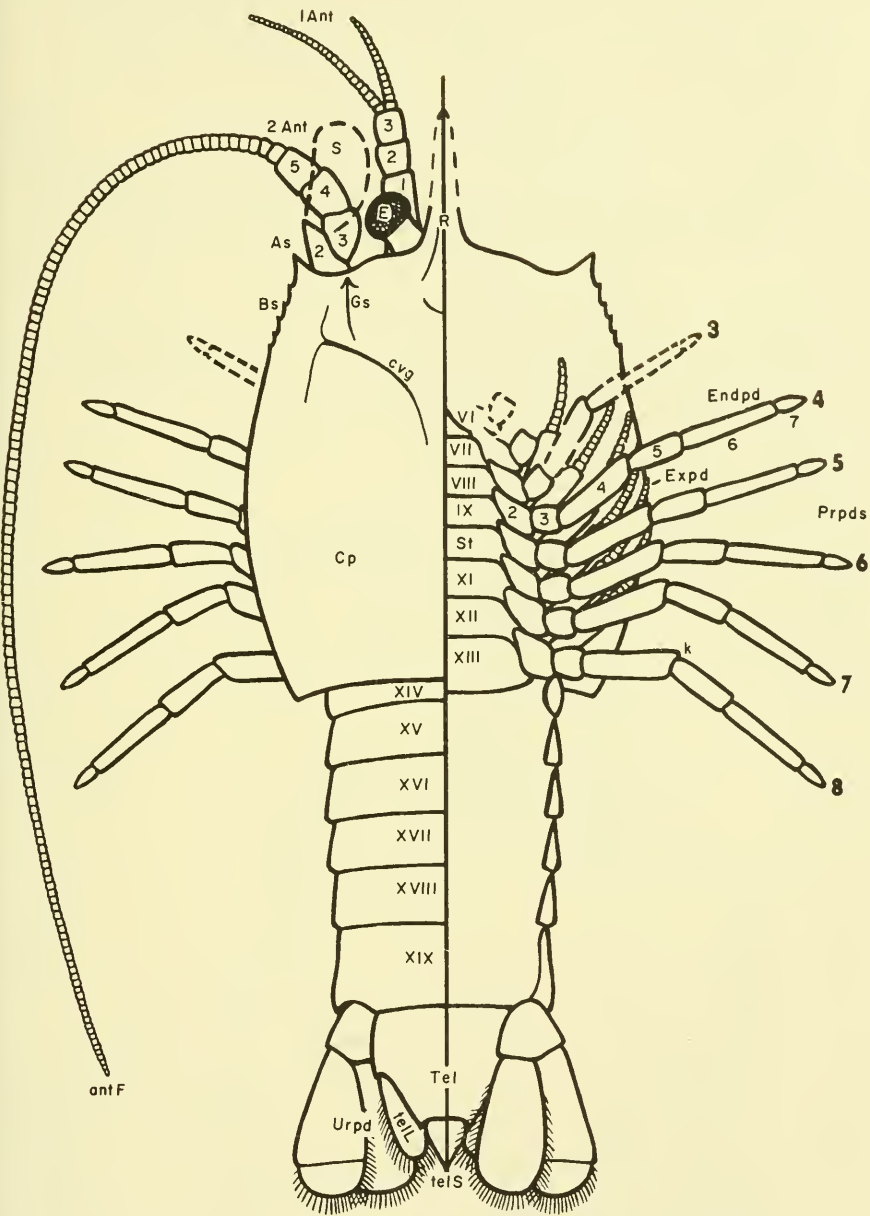
Explanation of Text Plate 4

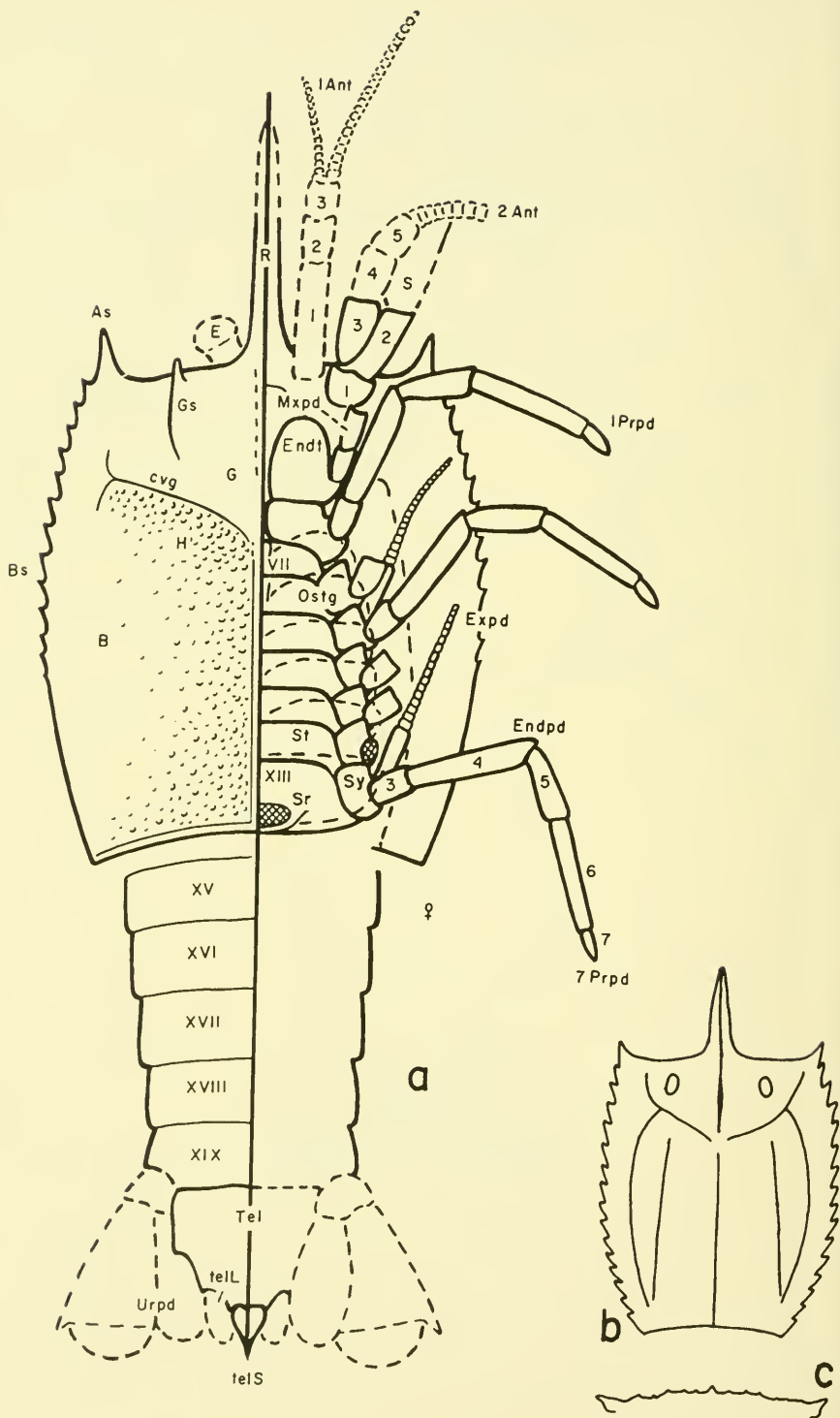
Figure

- a. Size frequency of the length of the body to specimens of *Anthracaris gracilis* (Meek and Worthen) presented as a histogram and a line graph. Statistical parameters for the population are given at the right.
- b. Anterior width of the carapace, maximum width of the carapace and the length of the rostrum of specimens of *A. gracilis* plotted relative to the length of the carapace of each individual as a scatter diagram to show allometric relationships.
- c. Size frequency of the length of the carapace of specimens of *A. gracilis* presented as a histogram. Statistical parameters for the population are given at the right.
- d. Scatter diagram showing variation in number of serrations relative to the body length of specimens of *A. gracilis*.

Explanation of Text Plate 5

| | Page |
|---|------|
| Mamayocaris jepseni n.g., n. sp. | 189 |
| Dorsal and ventral skeletal morphology of the left side diagram- matically drawn; X 6. | |



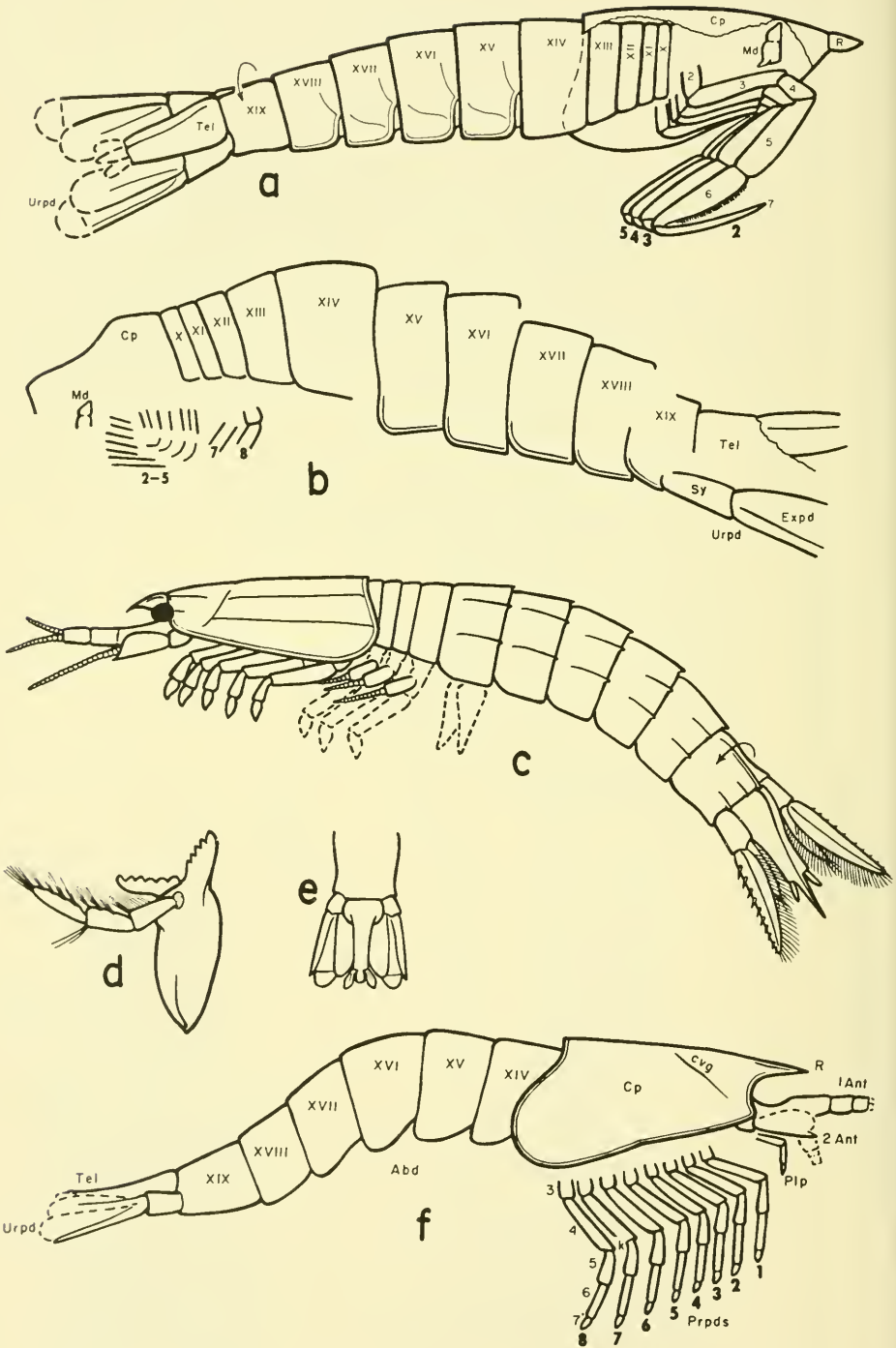


Explanation of Text Plate 6

| Figure | Page |
|---|------|
| a. Pygocephalus dubius (Milne-Edwards) | 194 |
| Dorsal and ventral skeletal morphology of the left side diagrammatically drawn. The oostegites shown by discontinuous lines would normally obscure the sternum in adult females; X 5. | |
| b. P. dubius | 194 |
| Drawing of carapace by Rhodes and Wilson (1957, text fig. 2). | |
| c. P. dubius | 194 |
| Median transverse section of carapace as interpreted by Rhodes and Wilson (1957, text fig. 2). | |

Explanation of Text Plate 7

| Figure | Page |
|--|------|
| a. Teallicaris loudonensis Peach | 200 |
| Dorsal and ventral skeletal morphology of the left side diagrammatically drawn; X 5. The oostegites shown by discontinuous lines would obscure the sternum in adult females. | |
| b. Pseudoteallicaris caudafimbriata (Copeland) | 200 |
| Dorsal features of the carapace; X 3. | |
| c. Teallicaris loudonensis Peach | 200 |
| Ventral features of cephalothorax as interpreted by Peach (1908, pl. 1, fig. 7 a) redrawn and simplified. | |

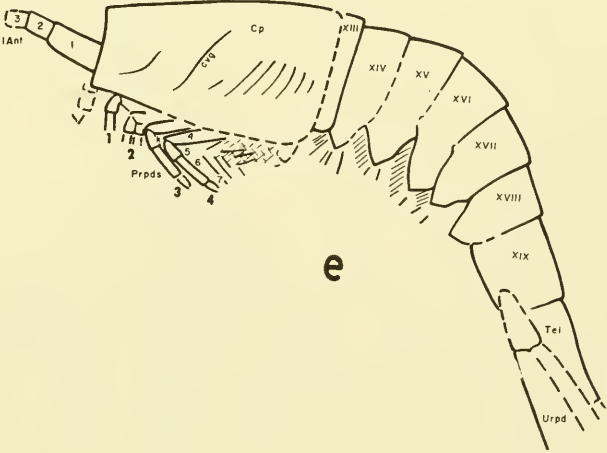
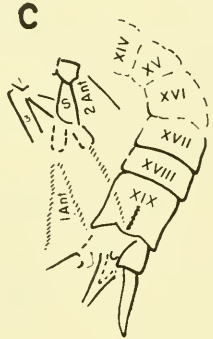
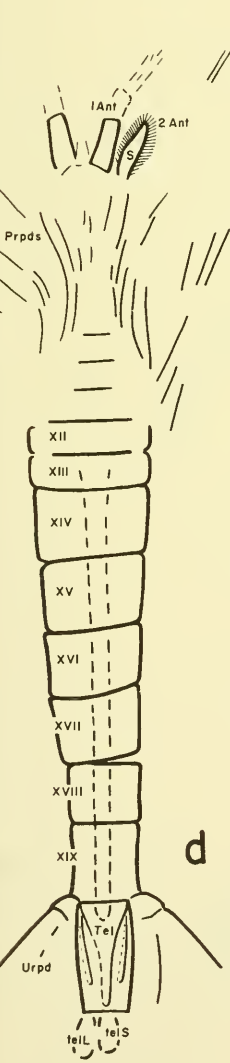
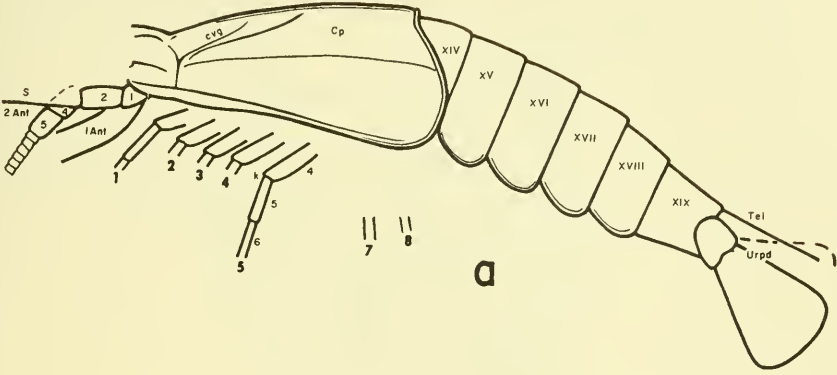


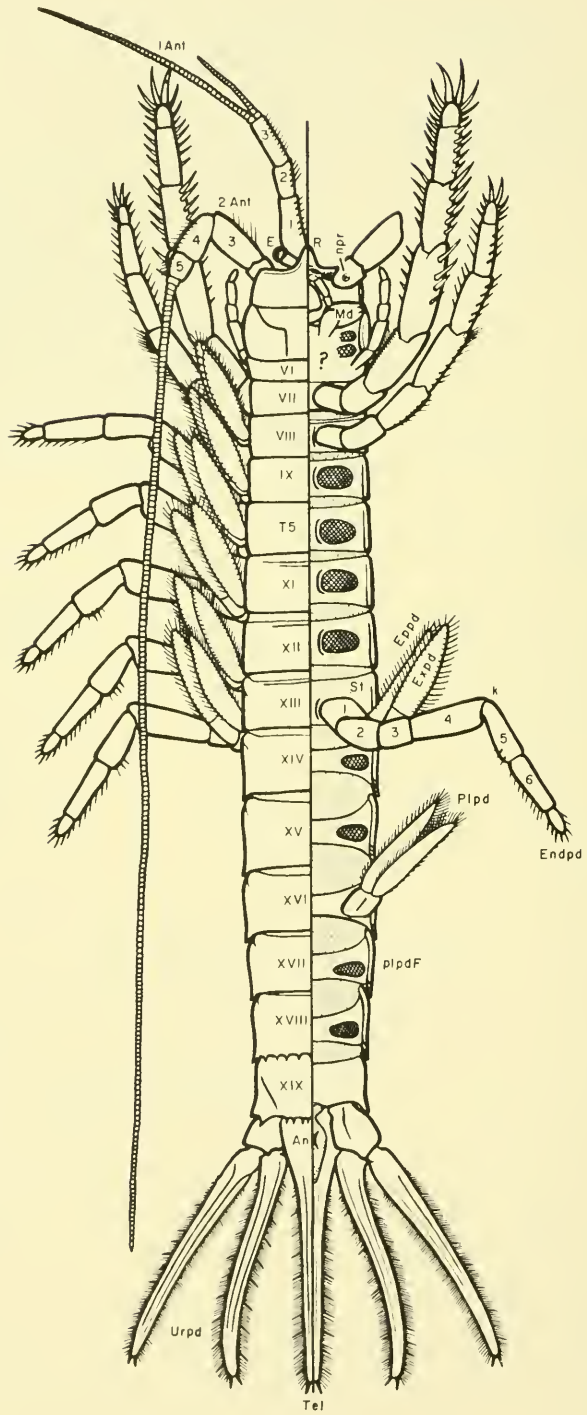
Explanation of Text Plate 8

| Figure | Page |
|---|------|
| a. Archaeocaris vermiformis Meek | 211 |
| Lateral restoration with portion of carapace removed to show known morphology of cephalothrax; X 3.5. | |
| b. A. graffhami , n. sp. | 214 |
| Diagrammatic drawing of holotype with morphological features identified; X 2.7. | |
| c. Perimecturus elegans Peach | 211 |
| Restoration based on characters illustrated by Peach (1908, pl. 6, figs. 2-6); X 2. | |
| d. Mandible of Recent specimen of Chloridella empusa (Say) | 213 |
| e. Caudal fan of Anthracophausia dunsiana Peach (1908, pl. 9, fig. 9). | 203 |
| f. Anthracophausia strongi , n. sp. | 203 |
| Lateral restoration; X 4. | |

Explanation of Text Plate 9

| Figure | Page |
|---|------|
| a. Palaeopalaemon newberryi Whitfield | 221 |
| Lateral restoration; X 2. | |
| b. Belotelson magister Packard | 206 |
| Diagrammatic drawing of Packard's plesiotype, USNM 38844; X 1. | |
| c. B. magister Packard | 206 |
| Diagrammatic drawing of the holotype, USNM 38844; X 1. | |
| d. Devonocaris cuylereensis (Wells) | 227 |
| Diagrammatic drawing of holotype, Cornell Univ. 40020; X 5. | |
| e. Eocaris oervigi Brooks | 172 |
| Diagrammatic drawing of holotype, Ar27335 in Swedish Museum of Natural History; X 3. | |





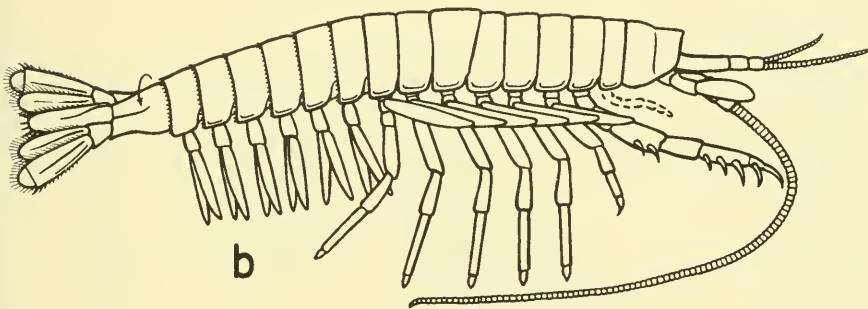
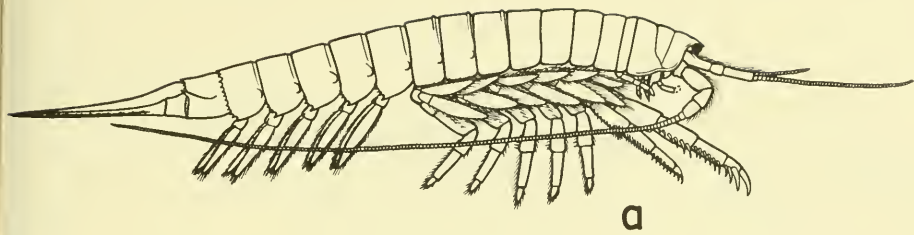
Explanation of Text Plate 10

Page

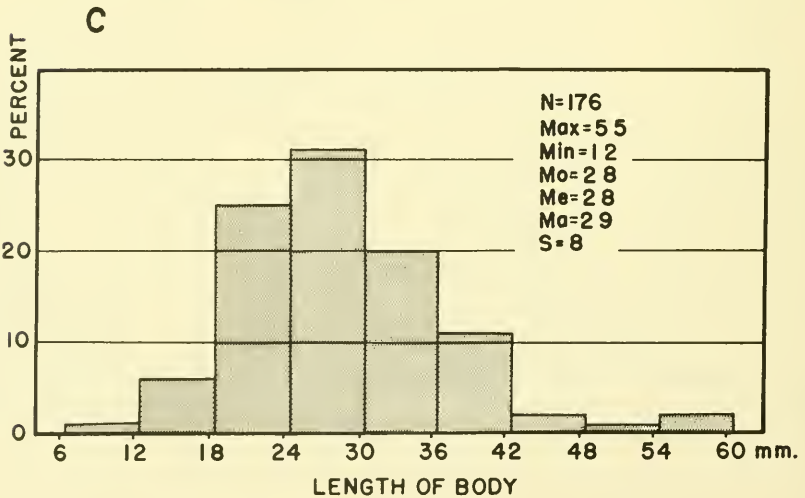
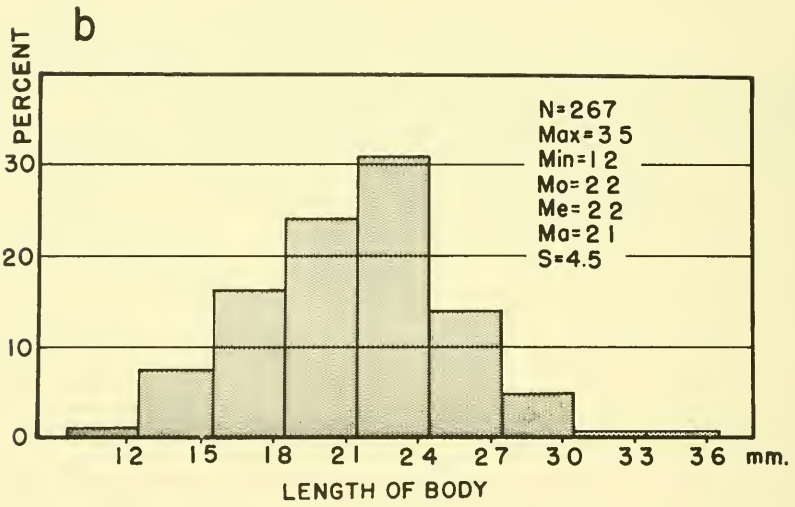
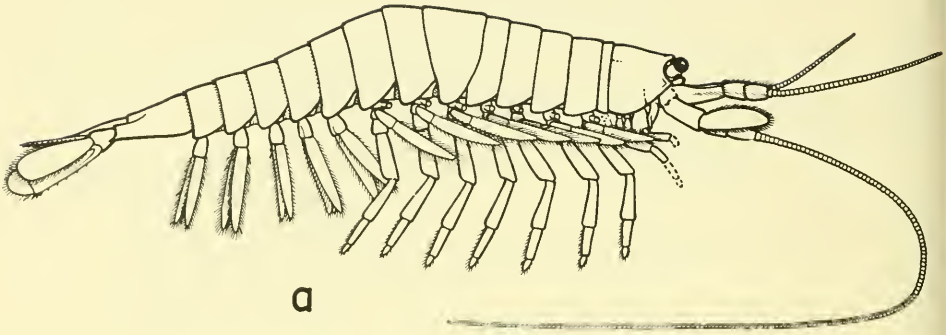
| | |
|---|-----|
| Acanthotelson stimpsoni Meek and Worthen | 230 |
| Dorsal and ventral skeletal morphology of the left side diagram- matically drawn; X 4. | |

Explanation of Text Plate 11

| Figure | Page |
|---|------|
| a. Acanthotelson stimpsoni Meek and Worthen Lateral restoration; X 2. | 230 |
| b. Uronectes fimbriatus (Jordan) Lateral restoration based upon specimens in the Museum of Comparative Zoology; X 3. | 230 |
| c. Table of measurements in millimeters of representative specimens of <i>Acanthotelson stimpsoni</i> Meek and Worthen and <i>Palaeocaris typus</i> Meek and Worthen. | |



| C | <i>Acanthatelsan stimpsoni</i> | | | | | | | <i>Palaeacaris typus</i> | | | | | | | |
|-----------------------|--------------------------------|---------|-------------|---------|--------------|---------|---------|--------------------------|-------------|---------|---------|---------|---------|---------|---------|
| | UI X-346 | PY19842 | MCZ 5210 | PY19821 | CMNH 4611 | PY19867 | PY19898 | USNN 38850 | MCZ 5197 | PY19731 | PY19734 | PY19755 | PY18850 | PY19728 | PY19734 |
| LENGTH OF BODY | 31 | 53 | 21 | 12 | 31 | 28 | 28 | 18 | 20 | 22 | 23 | 18 | 20 | 19 | 23 |
| LENGTH OF HEAD | 3 | 5 | 25 | 16 | 34 | 3 | 32 | 28 | 2 | 21 | 25 | 21 | 23 | 22 | 25 |
| LENGTH OF THORAX | 17 | 27 | 10 | 6 | 17 | 14 | 18 | 87 | 82 | 100 | 110 | 81 | | 87 | 106 |
| LENGTH OF 6th TH. T. | 20 | 38 | 17 | 14 | 22 | 19 | 20 | 28 | 19 | 23 | 24 | 21 | 23 | 18 | 24 |
| LENGTH OF 2nd ABD. T. | 22 | 37 | 17 | 14 | 19 | 19 | 20 | 12 | 10 | 11 | 13 | 07 | 17 | 13 | 13 |
| LENGTH OF 6th ABD. T. | 22 | 38 | 20 | 14 | 20 | 15 | 23 | 23 | 17 | 23 | 23 | 23 | 23 | 20 | 23 |
| LENGTH OF TELSON | 80 | | 72 | | | 80 | 86 | 35 | | | 37 | 32 | 45 | 31 | 32 |

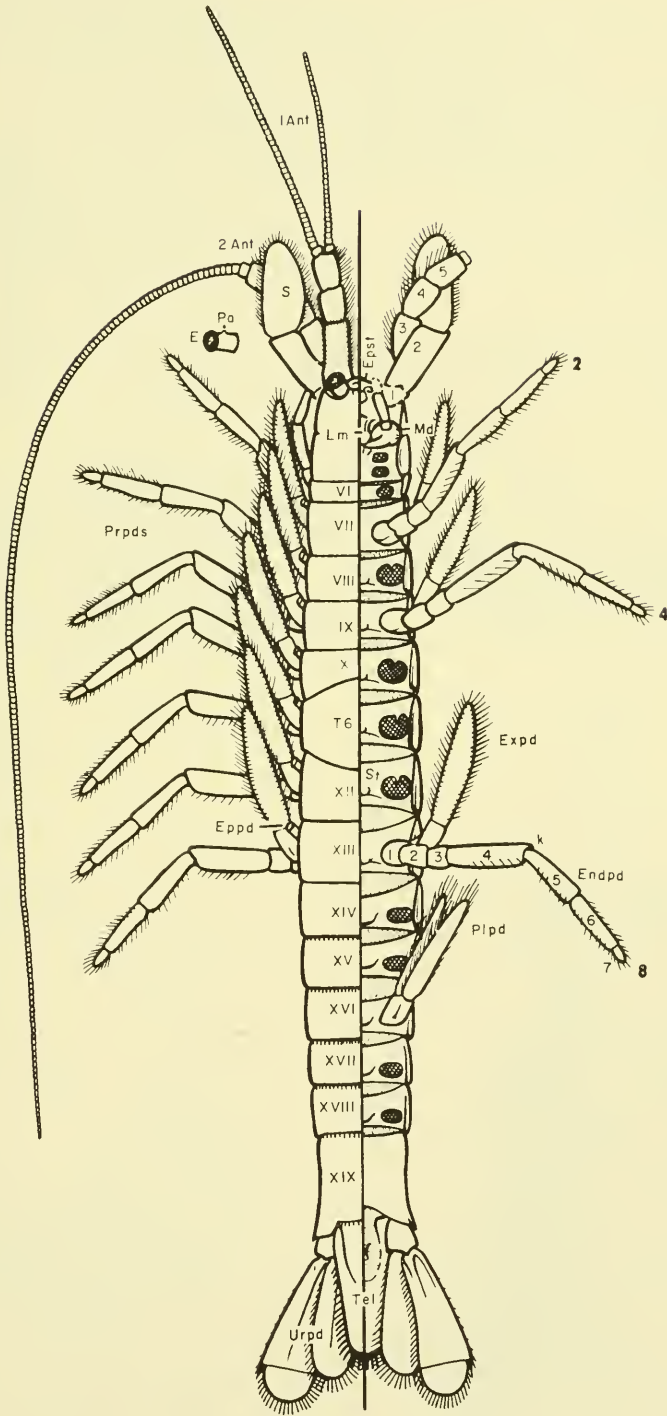


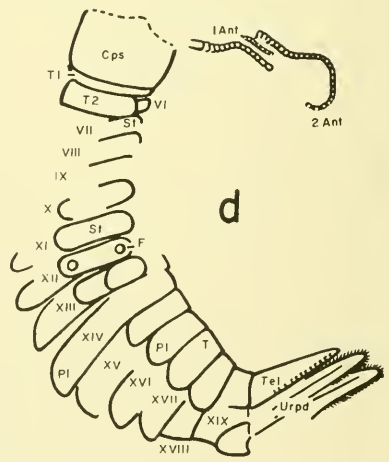
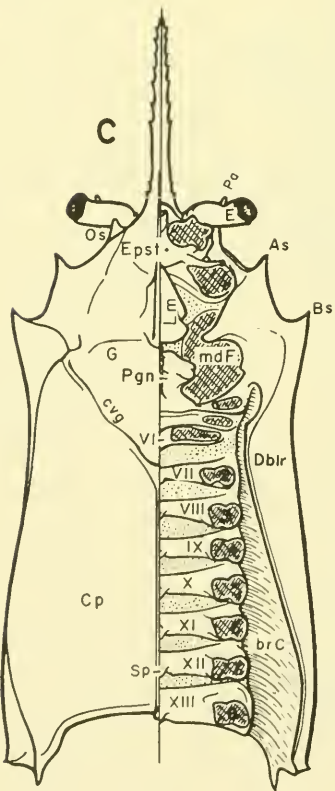
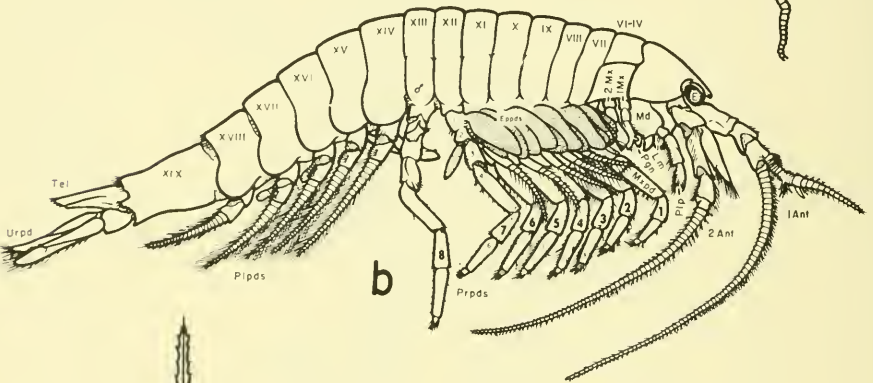
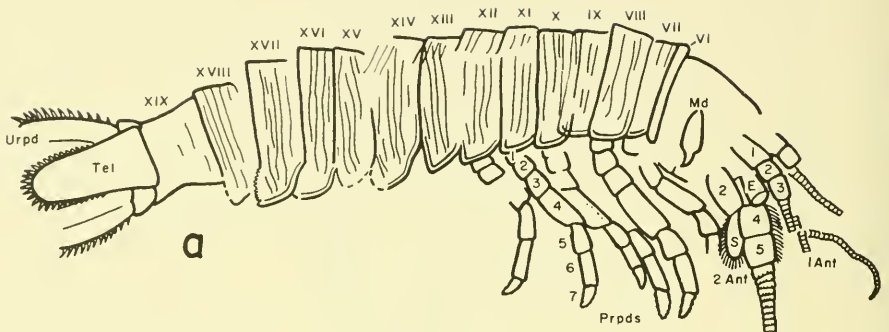
Explanation of Text Plate 12

| Figure | Page |
|---|------|
| a. Palaeocaris typus Meek and Worthen Lateral restoration; X 3. | 240 |
| b. Histogram of size frequency of the length of the body of specimens of <i>Palaeocaris typus</i> Meek and Worthen. | |
| c. Histogram of size frequency of the length of the body of specimens of <i>Acanthotelson simpsoni</i> Meek and Worthen. | |

Explanation of Text Plate 13

| | Page |
|--|------|
| Palaeocaris typus Meek and Worthen | 240 |
| Dorsal and ventral skeletal morphology of the left side diagrammatically drawn; X 5. | |



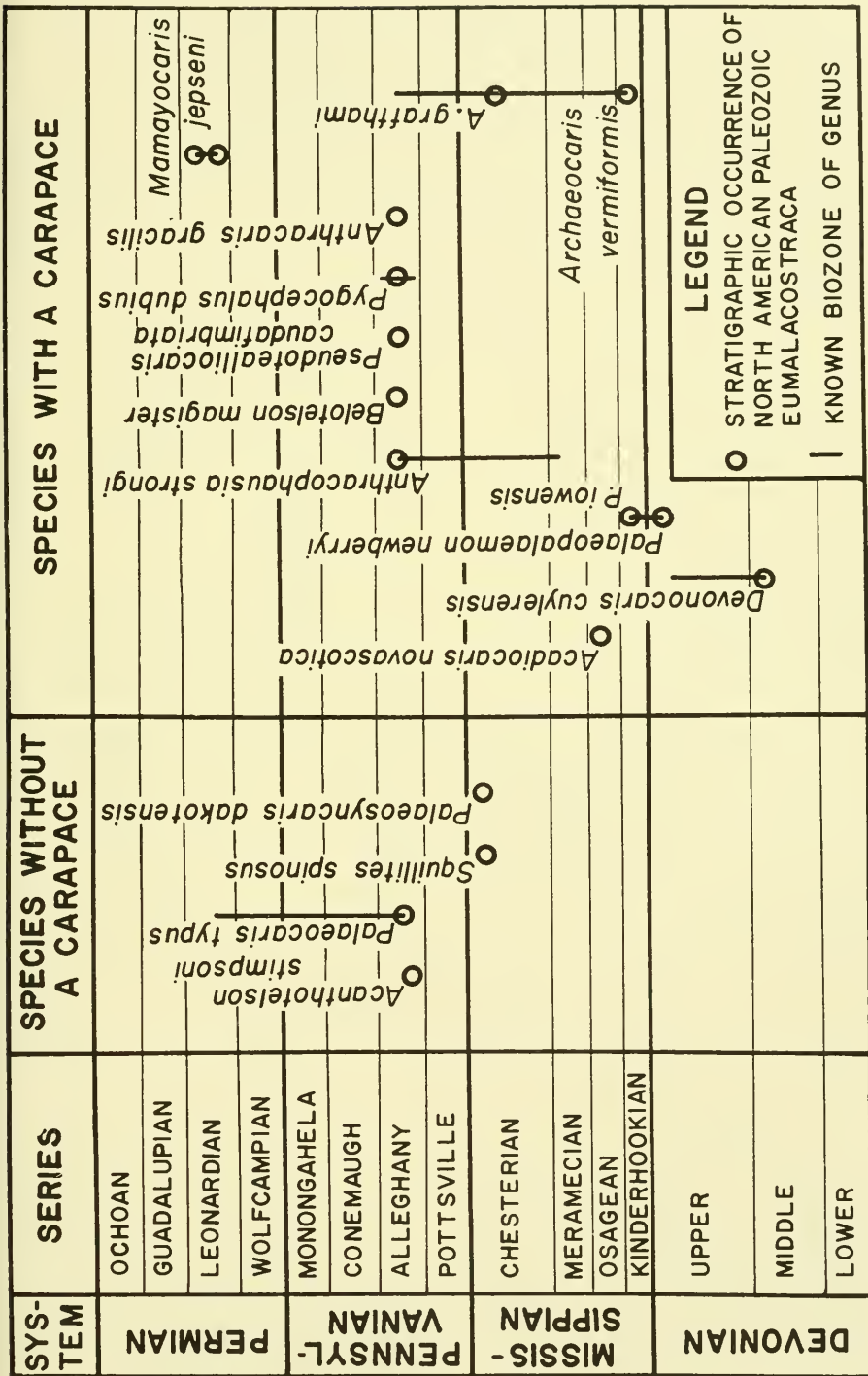


Explanation of Text Plate 14

| Figure | Page |
|--|------|
| a. Palaeosyncaris dakotensis , n.g., n. sp. | 251 |
| Diagrammatic drawing of the holotype; X 2. | |
| b. Anaspides tasmaniae (Thomson) | 170 |
| Skeletal morphology of Recent syncarid shown in lateral view; X 3. | |
| c. Gnathophausia gracilis Suhm | 170 |
| Dorsal and ventral skeletal morphology of cephalothorax of Recent lophogastrid mysidacean with appendages removed; X 3. | |
| d. Squillites spinosus Scott | 254 |
| Diagrammatic drawing of holotype; X 8. | |

Explanation of Text Plate 15

| | Page |
|--|------|
| Stratigraphic occurrence of Paleozoic Eumalacostraca of North America | 258 |



LEGEND

○ STRATIGRAPHIC OCCURRENCE OF NORTH AMERICAN PALEOZOIC EUMALACOSTRACA

— KNOWN BIOZONE OF GENUS

| SUPERORDERS OF RECENT EUMALACOSTRACA | EUCARIDA | PAN-CARIDA | PERACARIDA | | | | | | HOPLO-CARIDA | SYNCARIDA | | |
|--------------------------------------|-----------------|------------|------------------|---------------|-----------------------|-------------------|-------------|--------------|--------------|-------------|------------------------|--------------|
| ORDERS OF RECENT EUMALACOSTRACA | EUPHAUSI-ACEA | DECAPODA | THERMO-SBAENACEA | MYSIDACEA | TANAIDACEA | SPLEAEO-GRYPHACEA | CUMACEA | ISOPODA | AMPHIPODA | STOMATOPODA | BATHY-NELLACEA | ANASPIDACEA |
| Jur.-R. | | | | | | | | | | | | |
| Trias. | | | | Schim-perella | | | | Isopad-ites | | | | Anaspid-ites |
| Perm. | Palaeo-mpemphix | | Monrocaris | Notocaris | | | | | | | | Clarke-caris |
| Penn. | | | Anthracaris | Pygocephalus | O. PYGOCEPHALO-MORPHA | Anthracaris | Anthracaris | Archaeocaris | Parnecurus | | O. PALAEO-CARIDACEA | Palaeocaris |
| Miss. | Anthracophausia | | Tediilocaris | | | Anthracaris | | | | | O. PALAEO-STOMATO-PODA | Palaeocaris |
| Dev. | | | Palaeopalaemon | | O. EOCARIDACEA | Eocaris | | | | | | |

ORDERS OF PALEOZOIC EUMALACOSTRACA WITH REPRESENTATIVE GENERA CITED

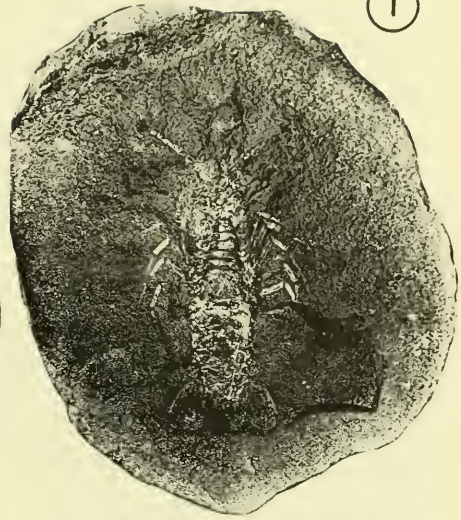
Explanation of Text Plate 16

| | Page |
|---|------|
| Diagram of the phylogenetic relationships of the Paleozoic Eumalacostraca | 264 |

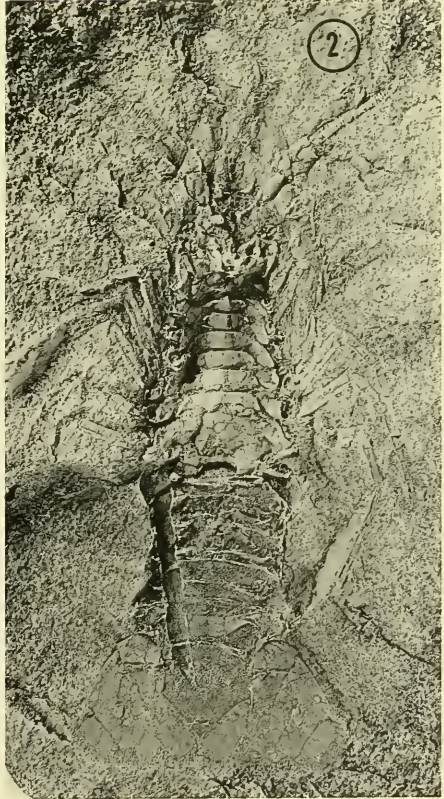
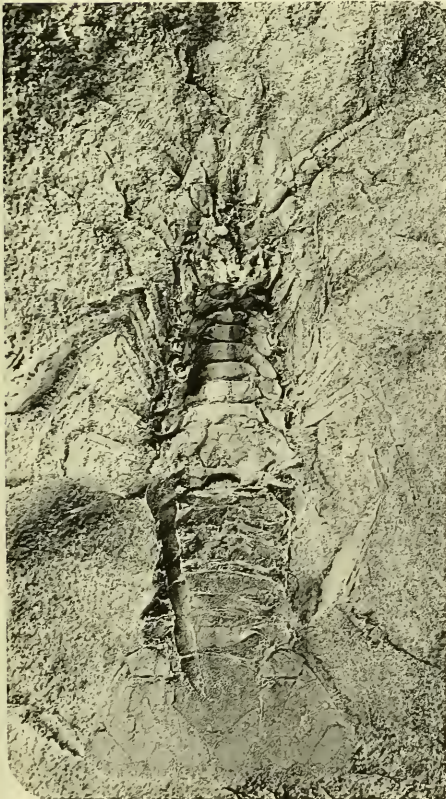
Explanation of Plate 29

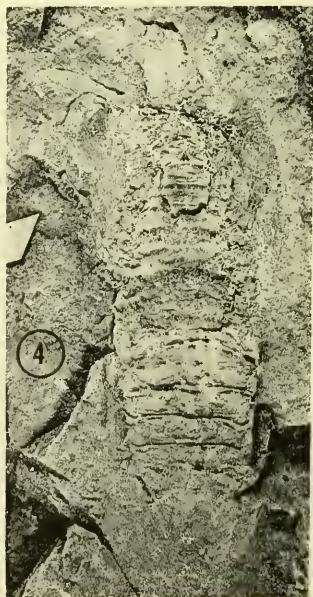
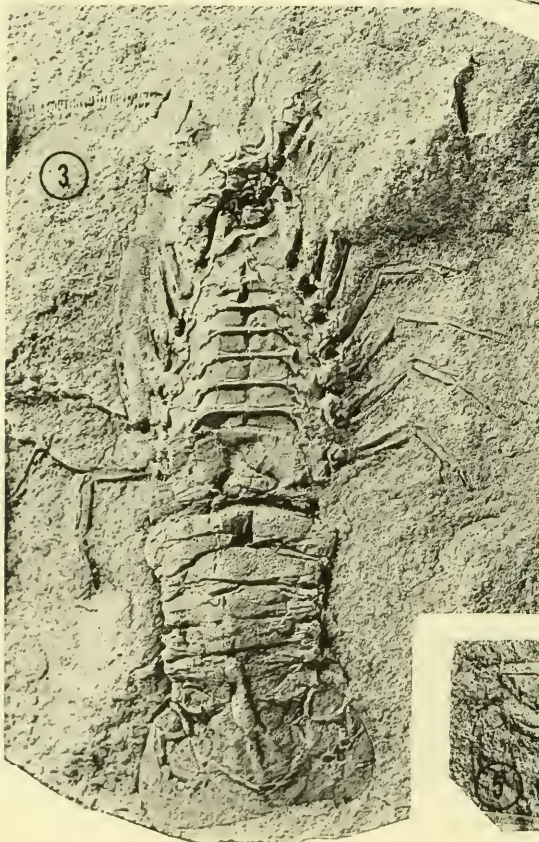
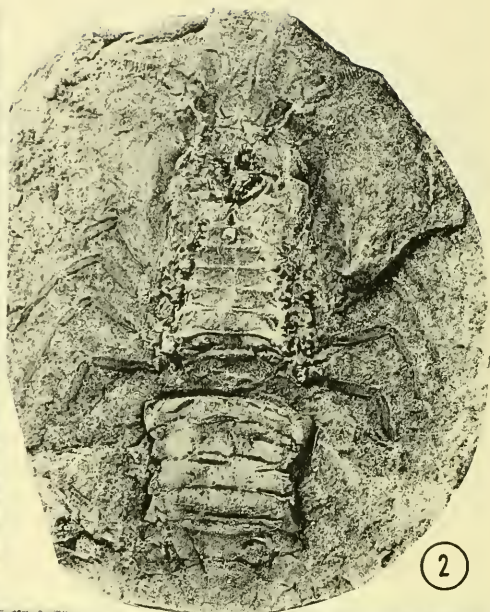
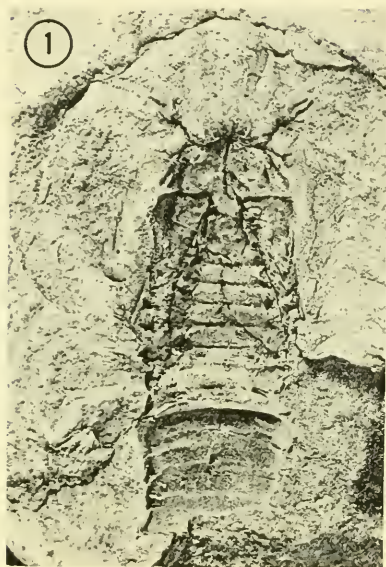
| Figure | Page |
|---|------|
| 1. Anthracaris gracilis (Meek and Worthen) Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19988. Ventral surface of specimen with natural mold partially filled with kaolin, X 1, stereograph. | 173 |
| 2. Same specimen but of rubber cast made after preparation, X 2.5, stereograph. | |

1



2



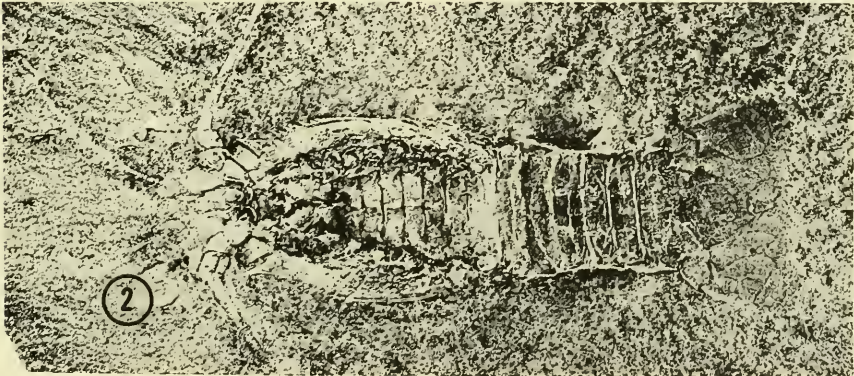
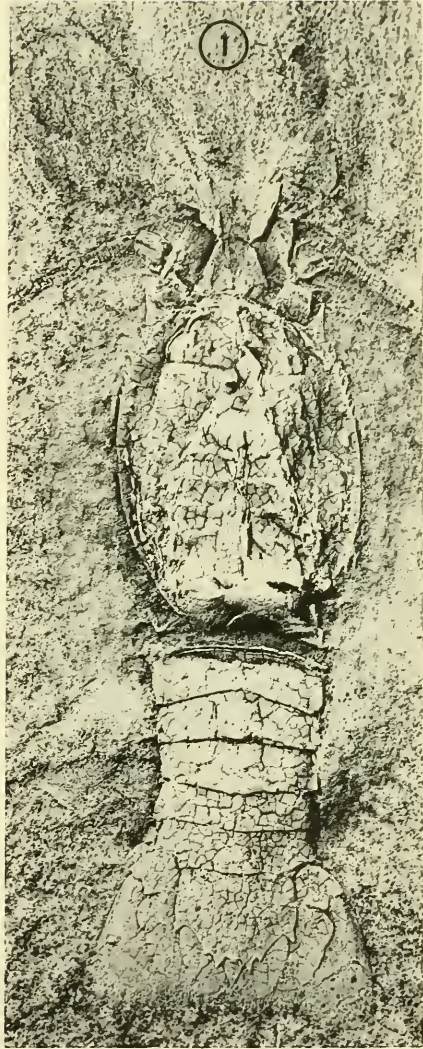
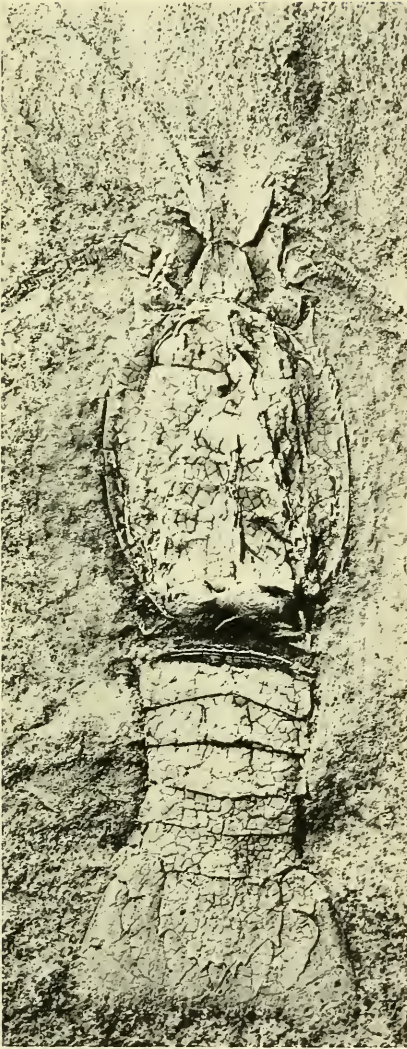


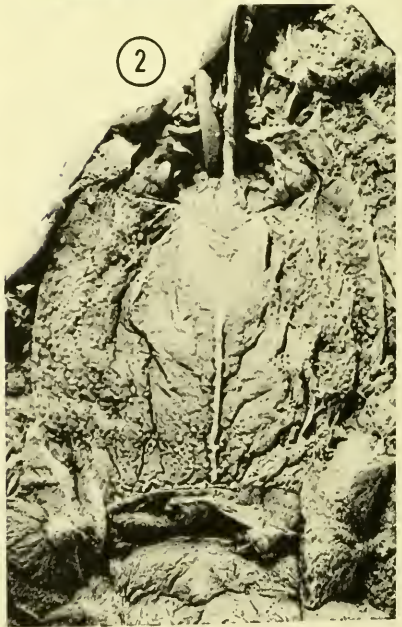
Explanation of Plate 30

| Figure | Page |
|--|------|
| 1. Anthracaris gracilis (Meek and Worthen) | 173 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., Ill. Geol. Survey (ISMNH 3067), holotype, X 3. | |
| 2. Counterpart, X 3. | |
| 3. A. gracilis | 173 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., USNM 38843, plesiotype of Packard (1886 c, pl. 7, fig. 4), X 3. | |
| 4. A. gracilis | 173 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., UI X-343, (ISMNH 11124), X 2. | |
| 5. A. gracilis | 173 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., USNM 38843, plesiotype of Packard (1886 c, pl. 7, fig. 3 a), X 2. | |

Explanation of Plate 31

| Figure | Page |
|--|------|
| 1. Anthracaris gracilis (Meek and Worthen) | 173 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19932, rubber cast, X 4, stereograph. | |
| 2. Counterpart, rubber cast, X 3. | |



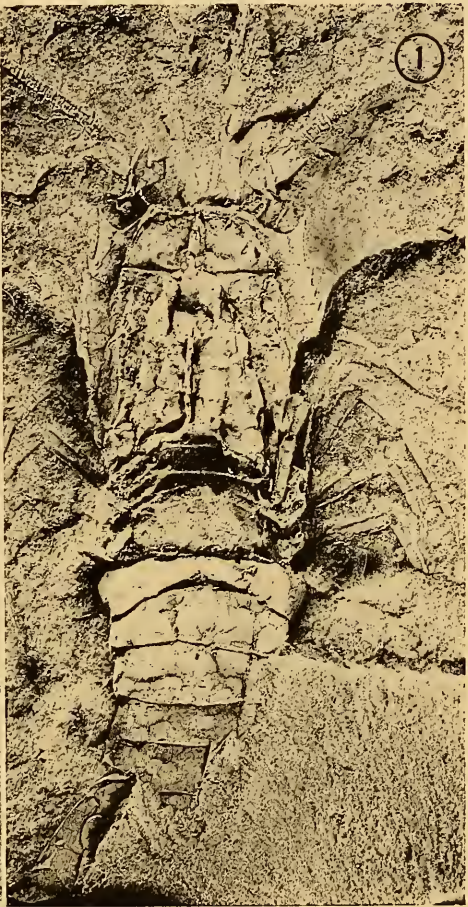
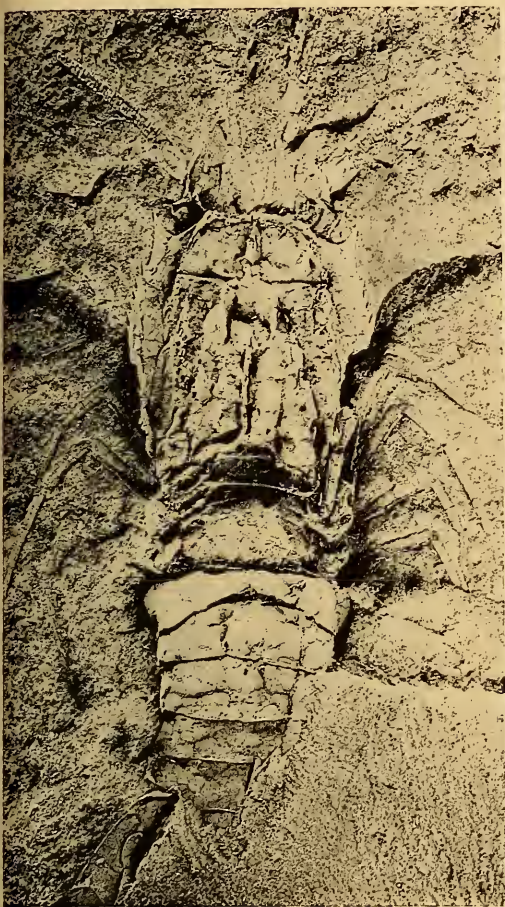


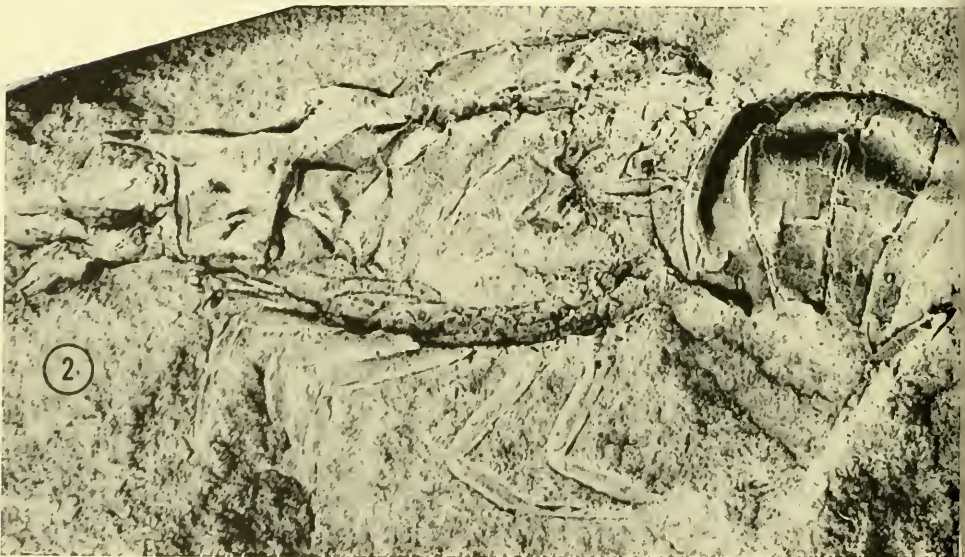
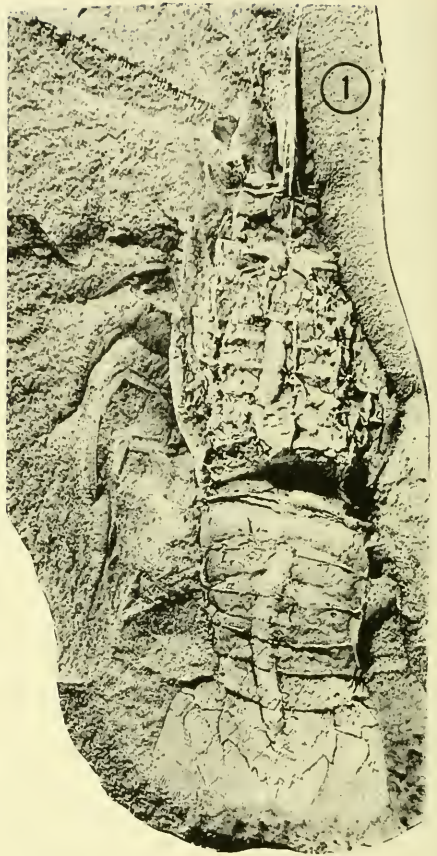
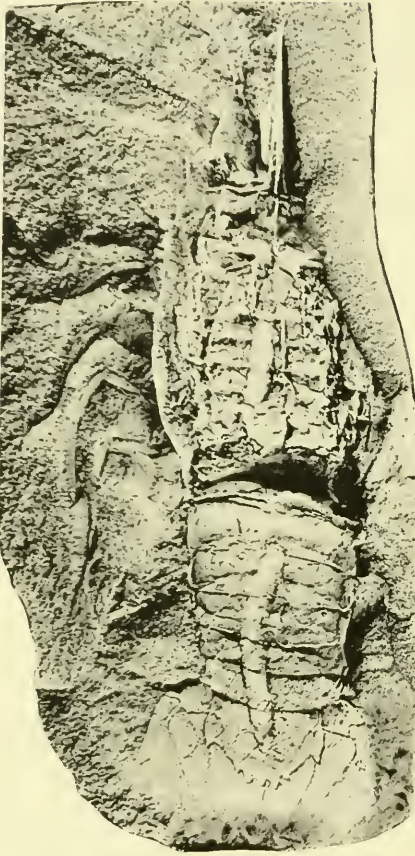
Explanation of Plate 32

| Figure | Page |
|--|------|
| 1. Anthracaris gracilis (Meek and Worthen) | 173 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 20003, rubber cast, X 3, stereograph. | |
| 2. A. gracilis | 173 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19975, rubber cast, X 4, stereograph. | |

Explanation of Plate 33

| Figure | Page |
|--|------|
| 1. Anthracaris gracilis (Meek and Worthen) | 173 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19988, rubber cast, X 3, stereograph. | |
| 2. A. gracilis | 173 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19941, X 4, stereograph. | |



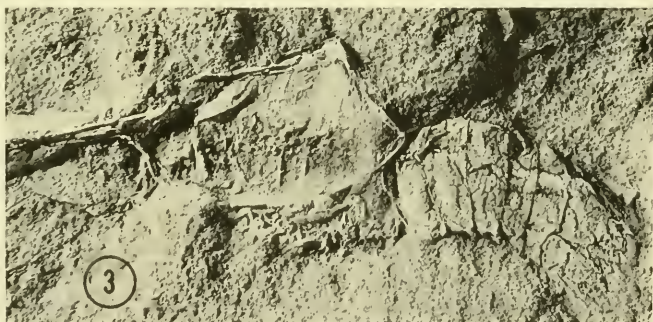
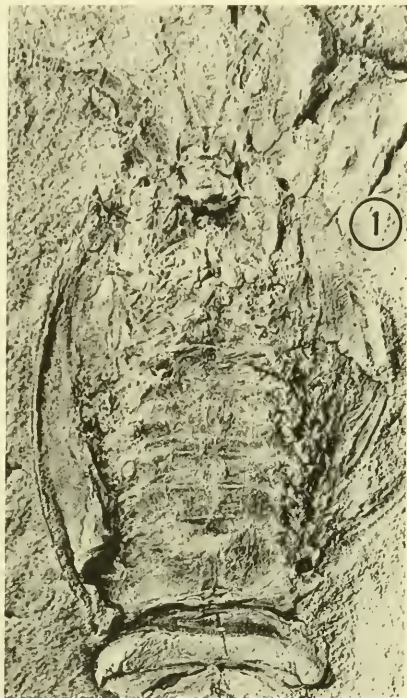
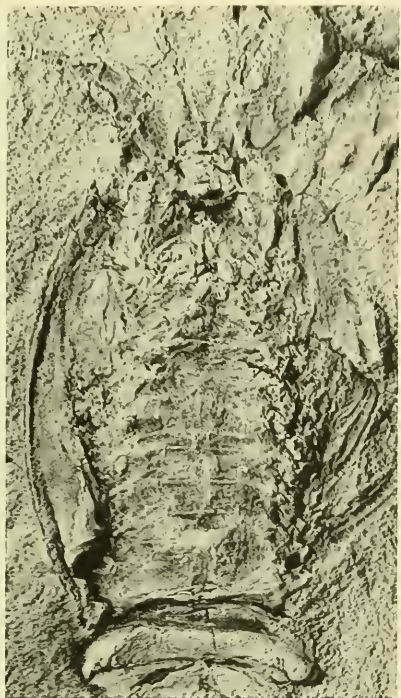


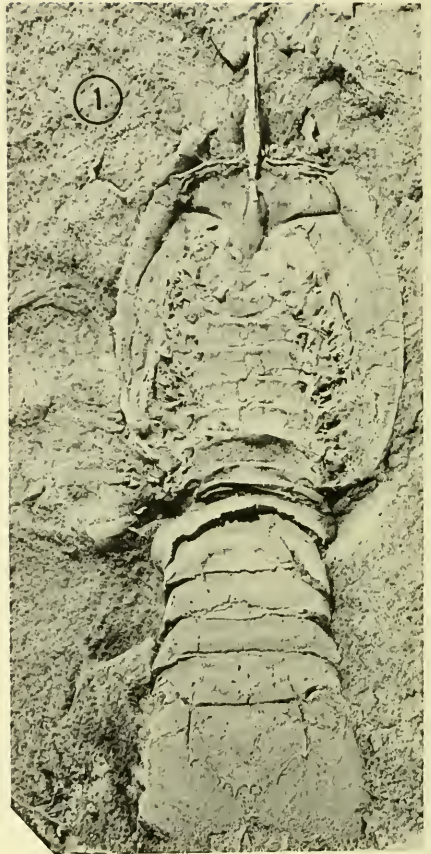
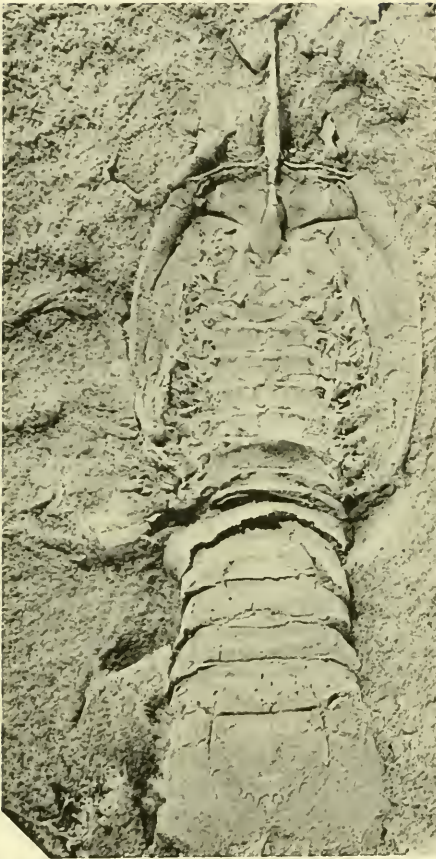
Explanation of Plate 34

| Figure | Page |
|--|------|
| 1. Anthracaris gracilis (Meek and Worthen) | 173 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19993, rubber cast, X 3, stereograph. | |
| 2. A. gracilis | 173 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 20005, X 6. | |

Explanation of Plate 35

| Figure | Page |
|--|------|
| 1. Anthracaris gracilis (Meek and Worthen) | 173 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19989, rubber cast, X 3, stereograph. | |
| 2. A. gracilis | 173 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19983, rubber cast, X 4. | |
| 3. A. gracilis | 173 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19928, rubber cast, X 2. | |
| 4. A. gracilis | 173 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19998, X 2. | |



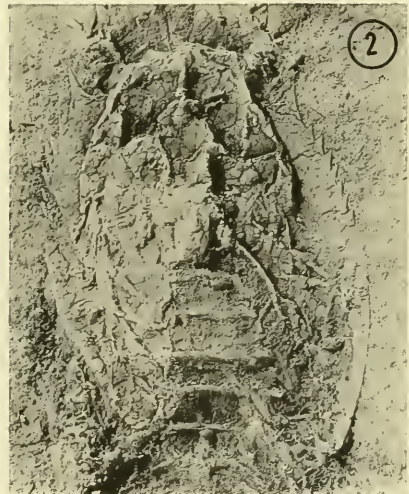
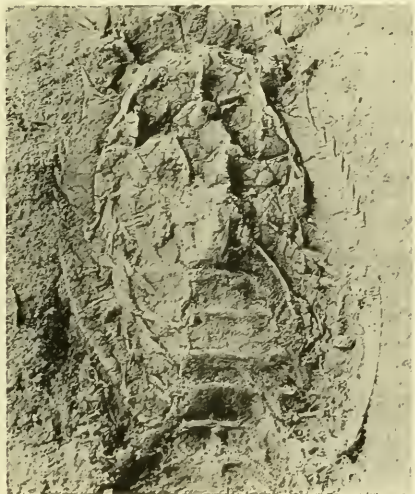
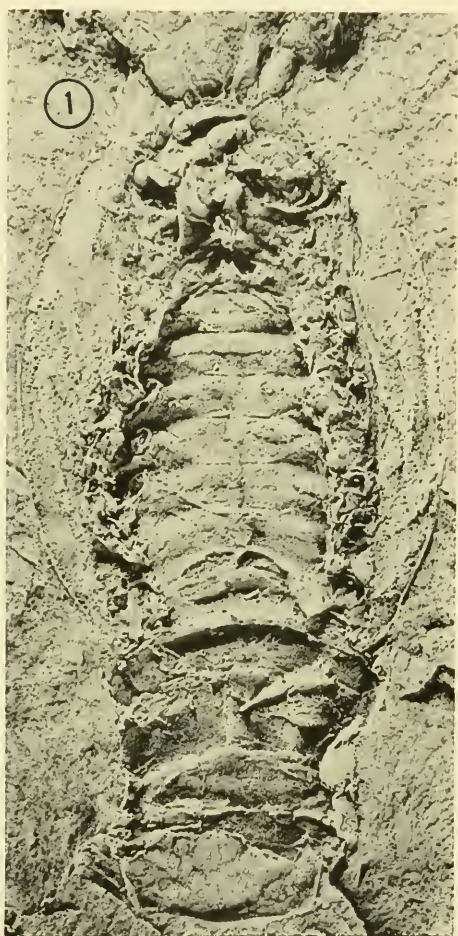
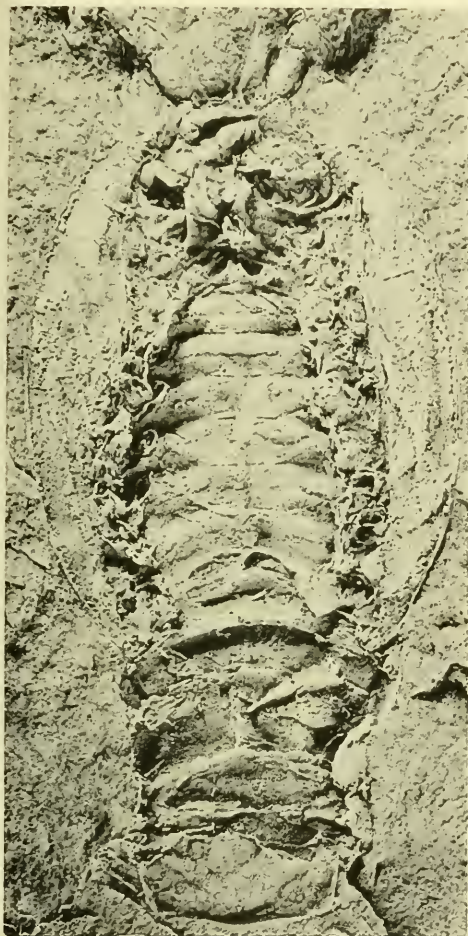


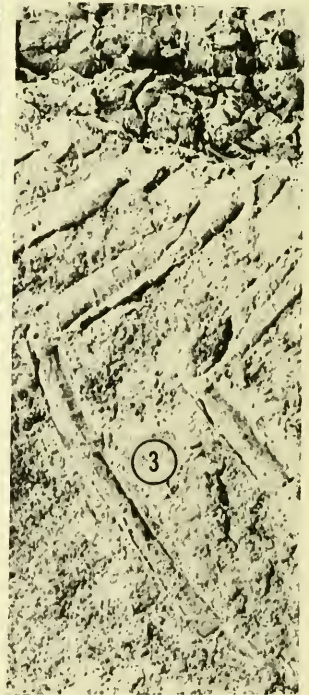
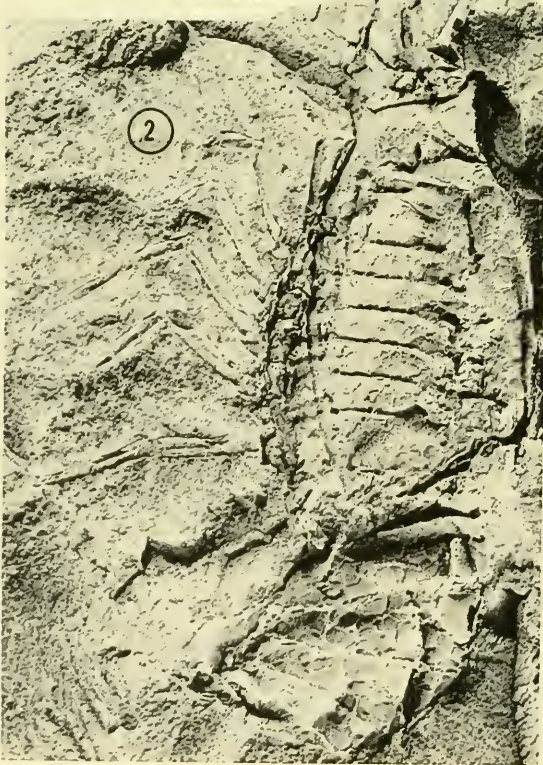
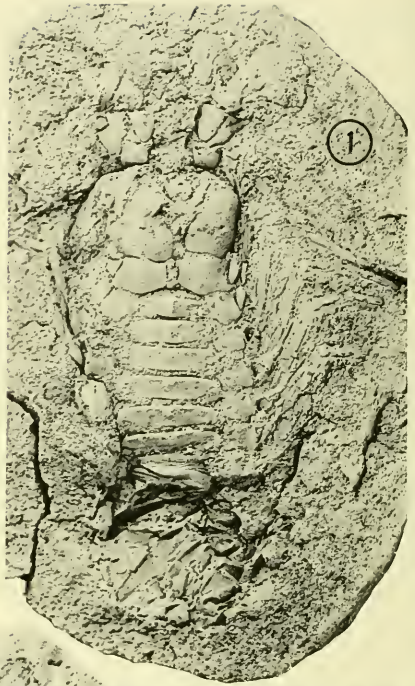
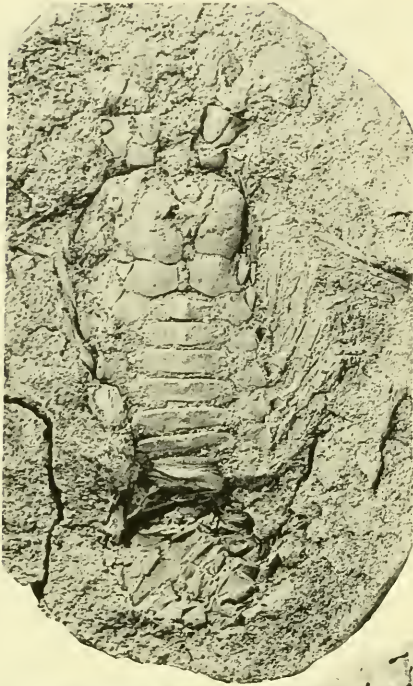
Explanation of Plate 36

| Figure | Page |
|--|------|
| 1. Anthracaris gracilis (Meek and Worthen) | 173 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19996 rubber cast, X 3, stereograph. | |
| 2. A. gracilis | 173 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19971, rubber cast, X 9, stereograph. | |

Explanation of Plate 37

| Figure | Page |
|--|------|
| 1. Anthracaris gracilis (Meek and Worthen) | 173 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19936, rubber cast, X 4, stereograph. | |
| 2. A. gracilis | 173 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19987, rubber cast, X 4, stereograph. | |



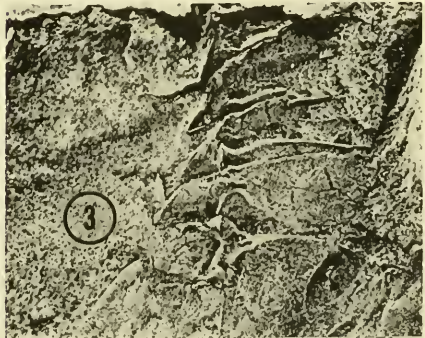
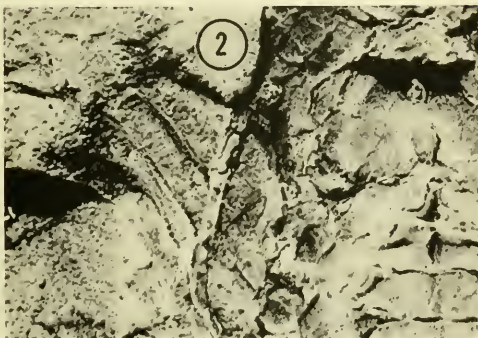
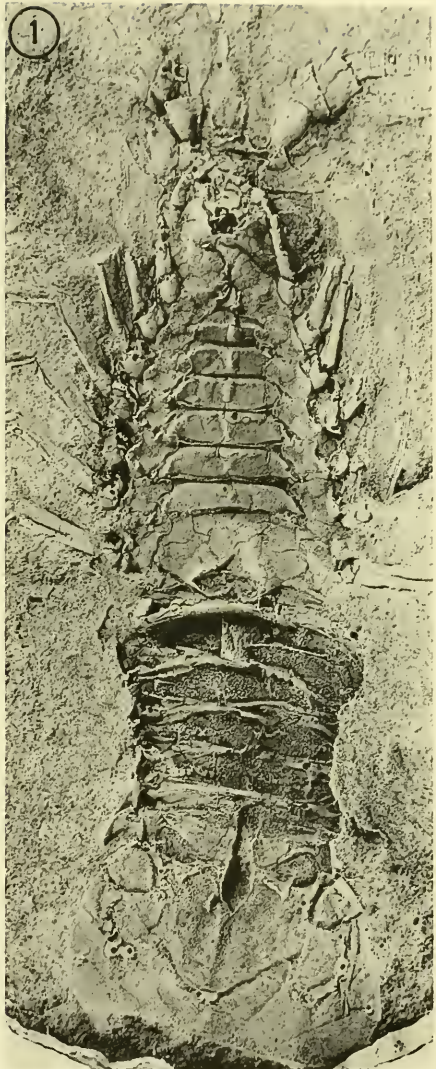
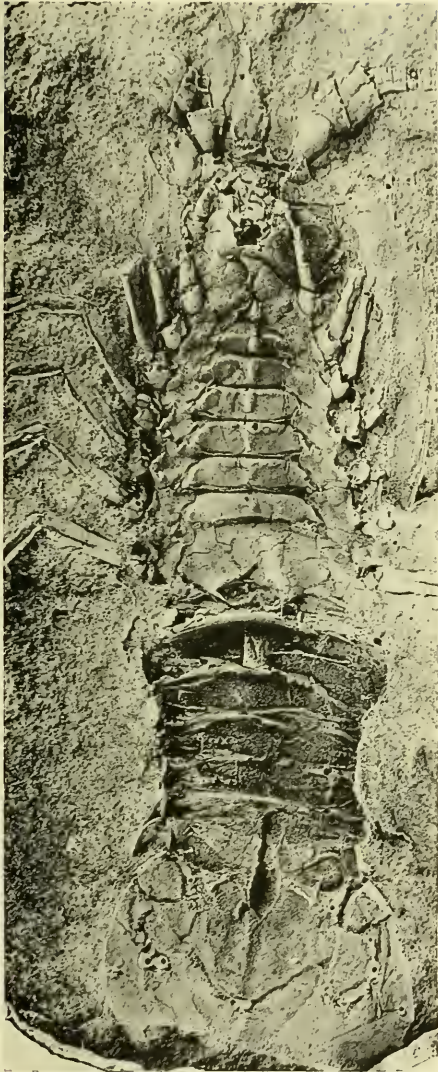


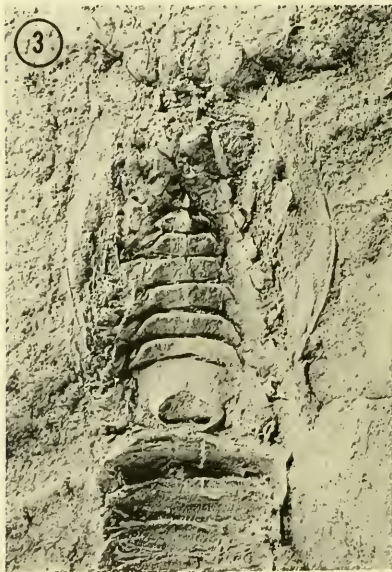
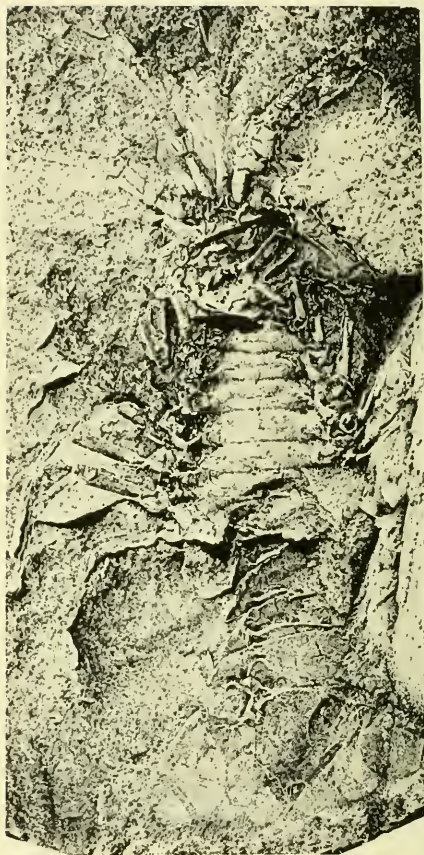
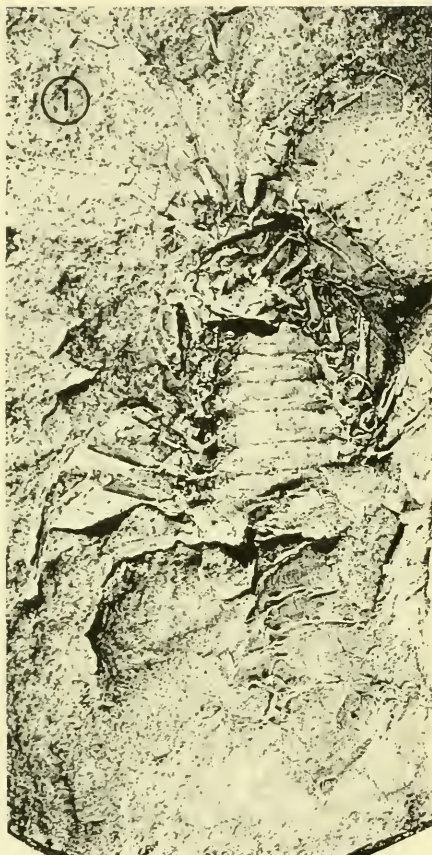
Explanation of Plate 38

| Figure | Page |
|---|------|
| 1. Pygocephalus dubius (Milne-Edwards) Pennsylvanian, England, MCZ 6718, X 4, stereograph. | 194 |
| 2. Anthracaris gracilis (Meek and Worthen) Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19953, X 4. | 173 |
| 3. Enlargement of photograph of same specimen showing the endopods, X 8. | |

Explanation of Plate 39

| Figure | Page |
|--|------|
| 1. Anthracaris gracilis (Meek and Worthen) | 173 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., USNM 38843, rubber cast, X 9, stereograph. | |
| 2. A. gracilis | 173 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19979, exopods, X 10. | |
| 3. A. gracilis | 173 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19931, rubber cast of abdominal pleurae, X 5. | |



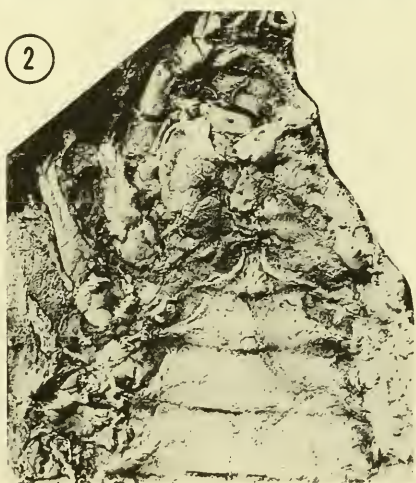
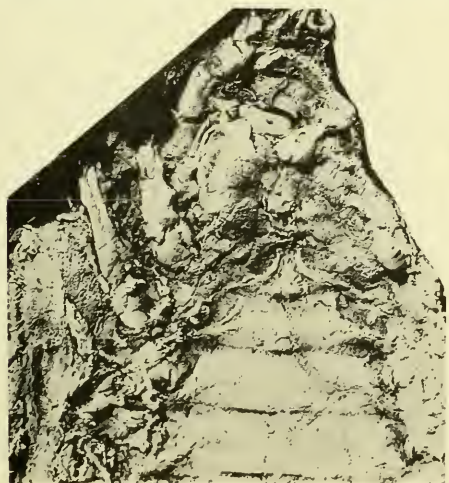
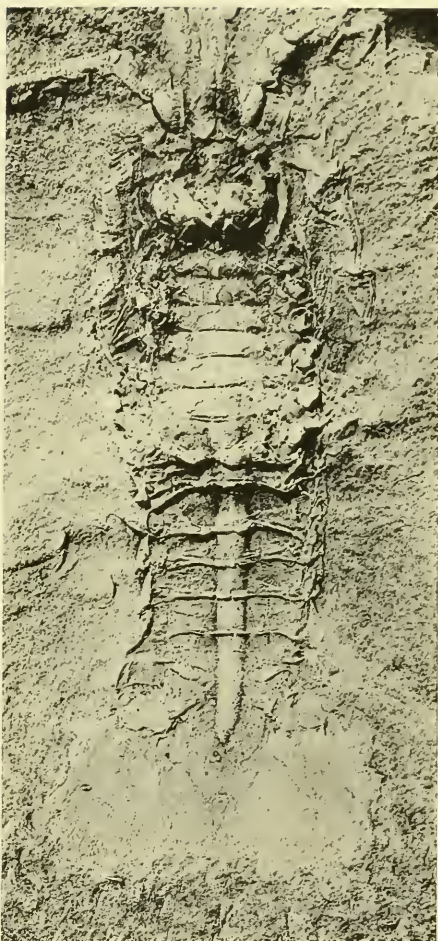
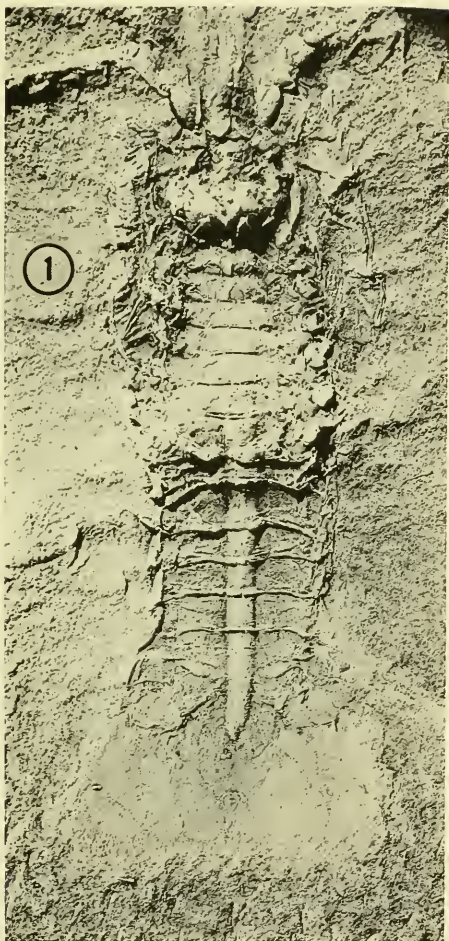


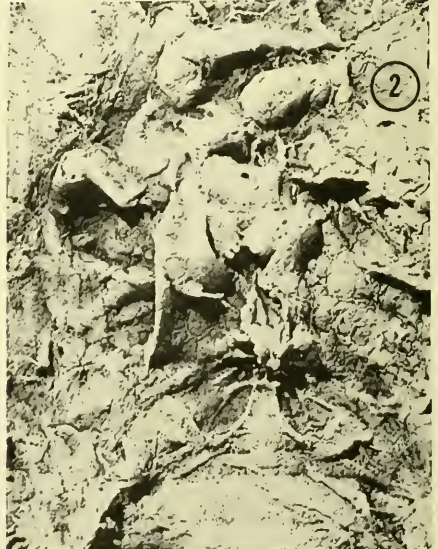
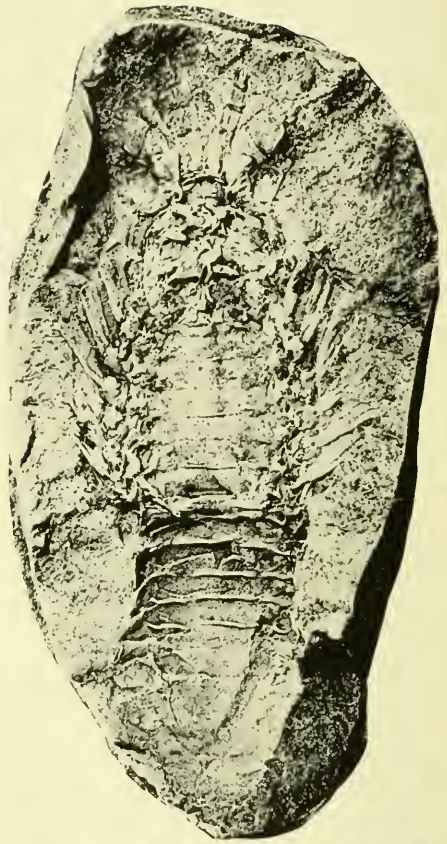
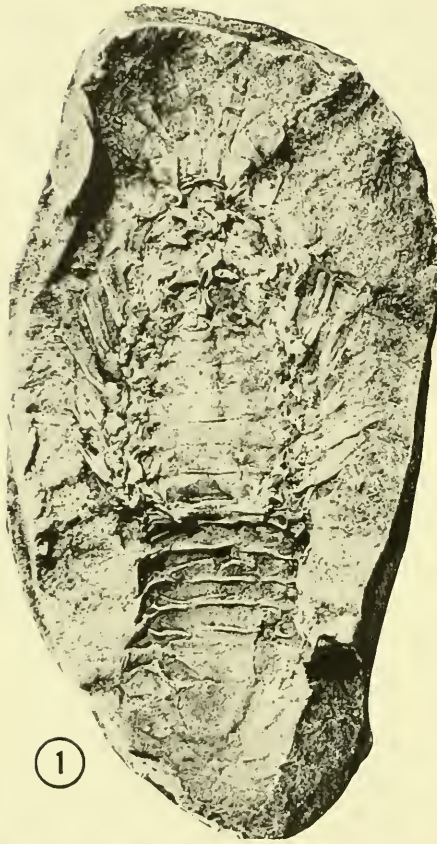
Explanation of Plate 40

| Figure | Page |
|--|------|
| 1. Anthracaris gracilis (Meek and Worthen) | 173 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19931, rubber cast, X 4, stereograph. | |
| 2. A. gracilis | 173 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19928, rubber cast of cephalothorax, X 3. | |
| 3. A. gracilis | 173 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19947, rubber cast of ventral surface showing sternites and seminal receptacle, X 4. | |

Explanation of Plate 41

| Figure | Page |
|---|------|
| 1. Anthracaris gracilis (Meek and Worthen) | 173 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., MCZ 5229, rubber cast, X 4, stereograph. | |
| 2. A. gracilis | 173 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19960, rubber cast of structures associated with the mouth, X 8, stereograph. | |



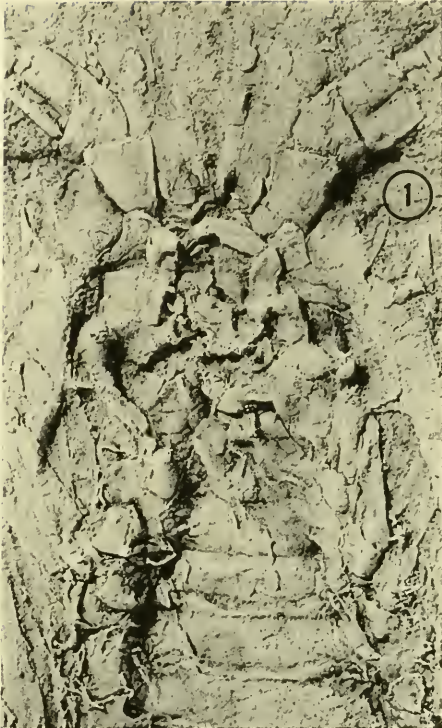


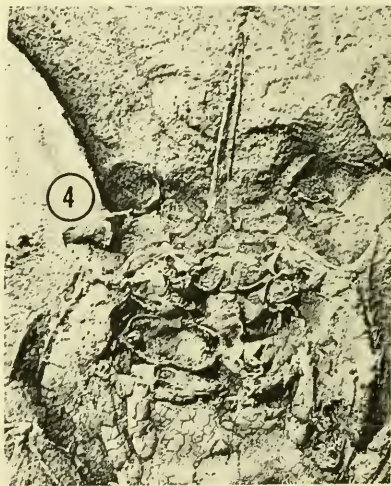
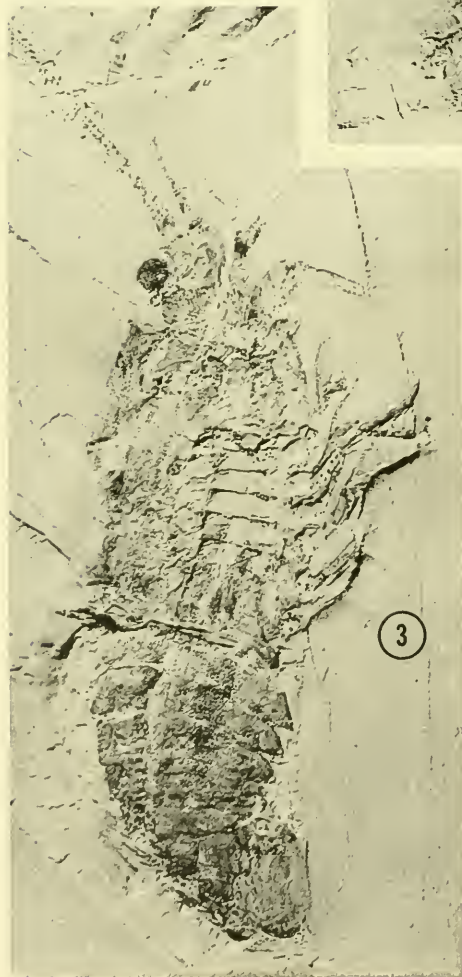
Explanation of Plate 42

| Figure | Page |
|---|------|
| 1. Anthracaris gracilis (Meek and Worthen) | 173 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 20022, rubber cast, X 3.5, stereograph. | |
| 2. A. gracilis | 173 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19936, rubber cast of structures associated with the mouth, X 8, stereograph. | |

Explanation of Plate 43

| Figure | Page |
|---|------|
| 1. Anthracaris gracilis (Meek and Worthen) Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19929, rubber cast of ventral structure of cephalothorax X 7, stereograph. | 173 |
| 2. A. gracilis Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19988, rubber cast of ventral structure of cephalothorax, X 6, stereograph. | 173 |



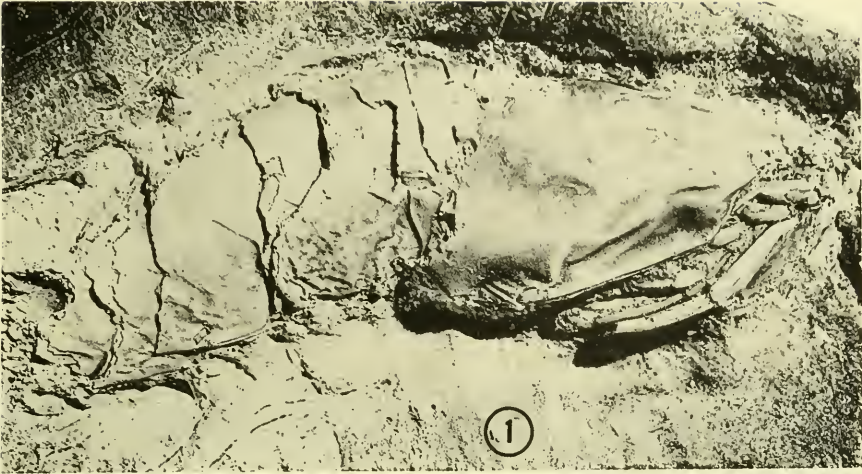


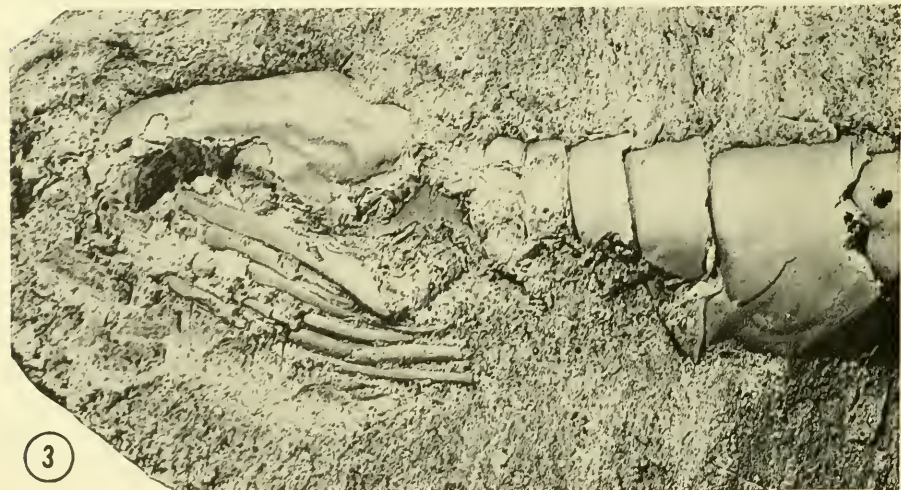
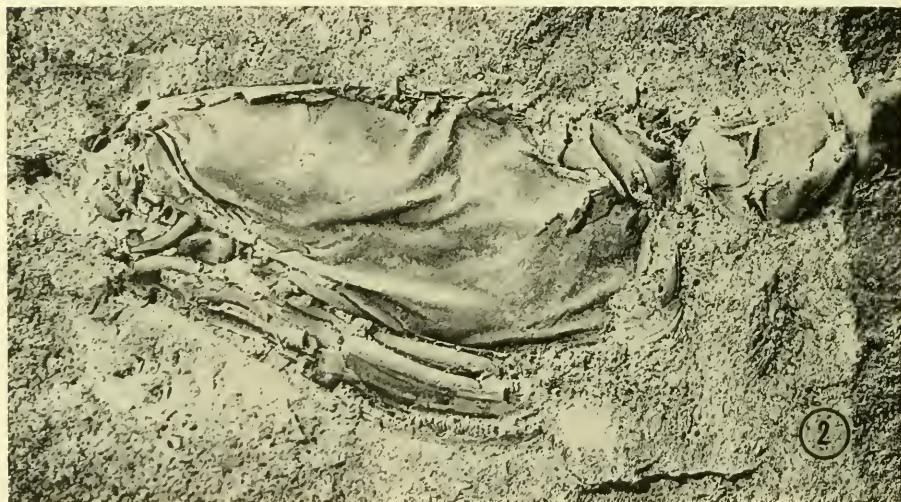
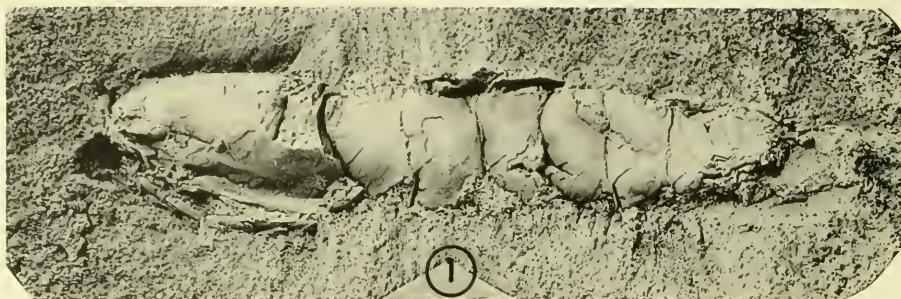
Explanation of Plate 44

| Figure | Page |
|--|------|
| 1. Mamayocaris jepseni , n.g., n.sp. | 189 |
| Vale fm., Permian, Taylor Co., Texas, USNM 133393, abdominal pleurae, X 5. | |
| 2. Mamayocaris jepseni | 189 |
| Vale fm., Permian, Taylor Co., Texas, USNM 133393, holotype, X 6. | |
| 3. Counterpart of holotype, X 5. | |
| 4. Anthracaris gracilis (Meek and Worthen) | 173 |
| Francis Creek, Grundy Co., Ill., USNM 38842, rubber cast of ventral features of head, X 5. | |

Explanation of Plate 45

| Figure | Page |
|---|------|
| 1. Archaeocaris vermiformis Meek | 211 |
| New Providence fm., Mississippian, Linietta Springs, Boyle Co., Ky., PU 1597 ^d /3, X 6. | |
| 2. Archaeocaris vermiformis | 211 |
| New Providence fm., Mississippian, Linietta Springs, Boyle Co., Ky., PU 1597 ^d /3, articulated rostrum, X 10. | |
| 3. Archaeocaris vermiformis | 211 |
| New Providence fm., Mississippian, Linietta Springs, Boyle Co., Ky., PU 1597 ^d /4, caudal fan, X 5. | |
| 4. Archaeocaris vermiformis | 211 |
| New Providence fm., Mississippian, Linietta Springs, Boyle Co., Ky., PU 1597 ^d /5, mandible, X 10. | |
| 5. Mamayocaris jepсени , n.g., n.sp. | 189 |
| Opeche fm., Permian, Rapid City, S.D., PU 83463 a, paratype, X 7. | |



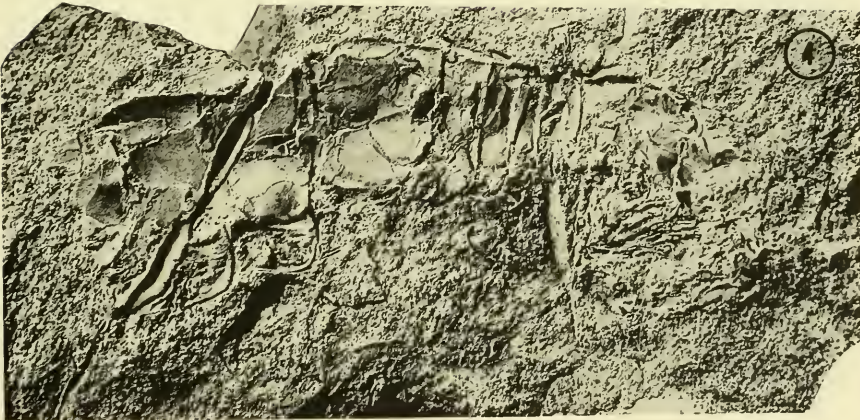
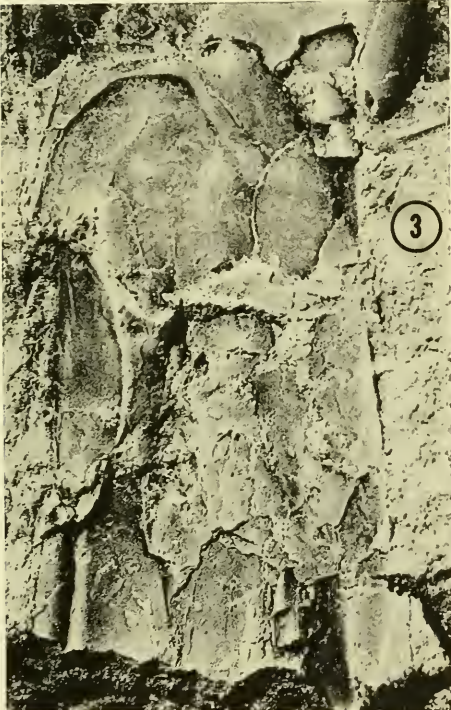
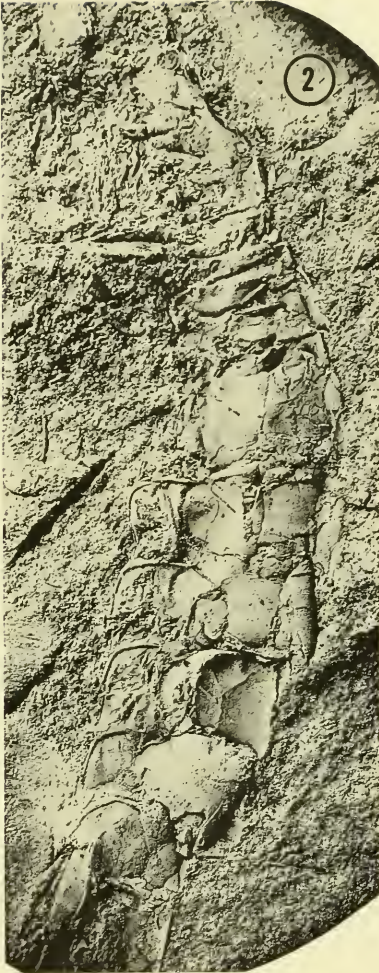
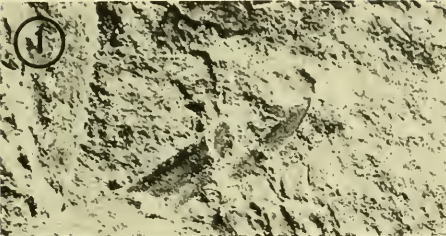


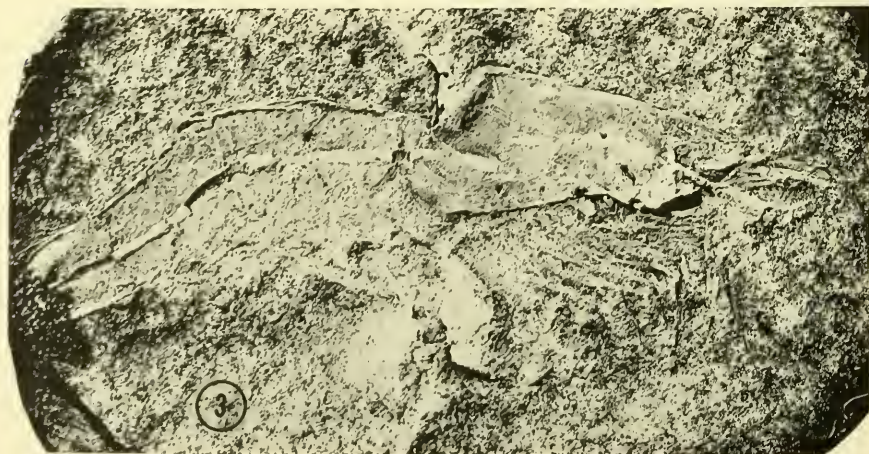
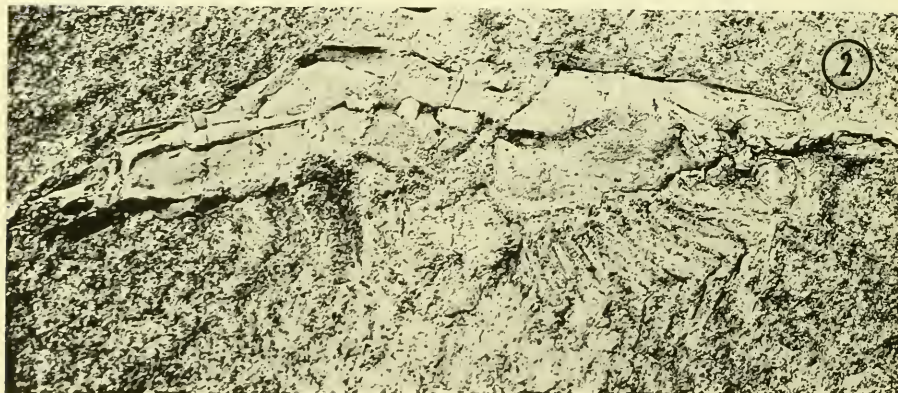
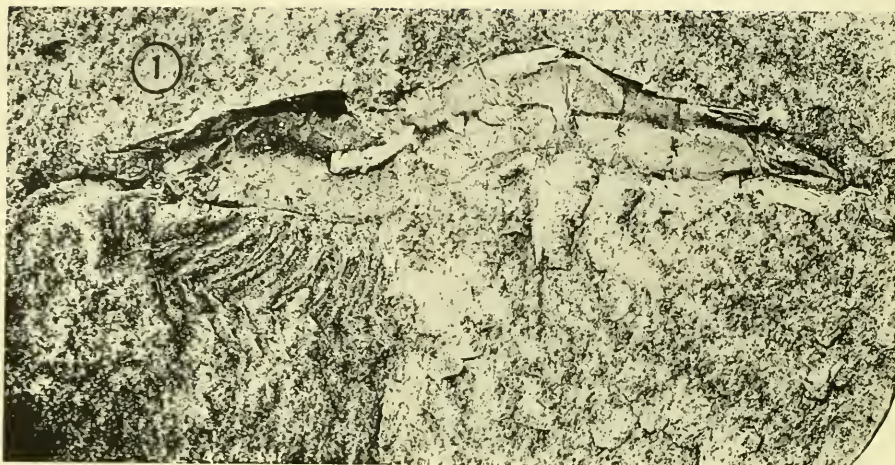
Explanation of Plate 46

| Figure | Page |
|---|------|
| 1. Archaeocaris vermiformis Meek | 211 |
| New Providence fm., Mississippian, Linietta Springs, Boyle Co., Ky., USNM 27126, holotype, X 4. | |
| 2. Archaeocaris vermiformis | 211 |
| New Providence fm., Mississippian, Linietta Springs, Boyle Co., Ky., PU 1597 ^d /1, X 8. | |
| 3. Archaeocaris vermiformis | 211 |
| New Providence fm., Mississippian, Linietta Springs, Boyle Co., Ky., PU 1597 ^d /2, X 8. | |

Explanation of Plate 47

| Figure | Page |
|---|------|
| 1. Archaeocaris graffhami , n. sp. 5879 | 214 |
| Caney shale Mississippian, Pontotoc Co., Okla., MCZ 5849, remnants of posterior thoracic legs. X 10. | |
| 2. Archaeocaris graffhami , n. sp. | 214 |
| Caney shale, Mississippian, Pontotoc Co., Okla., MCZ 5849, holotype, X 4. | |
| 3. Caudal fan of holotype, X 10. | |
| 4. Counterpart of holotype UO 4411, X 4. | |



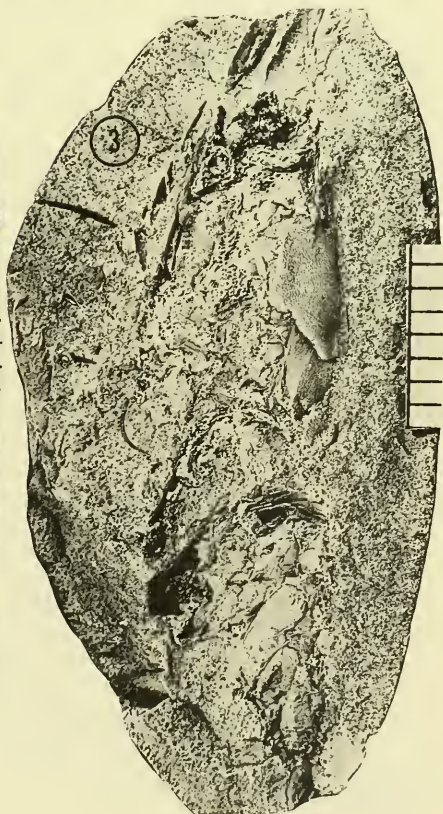
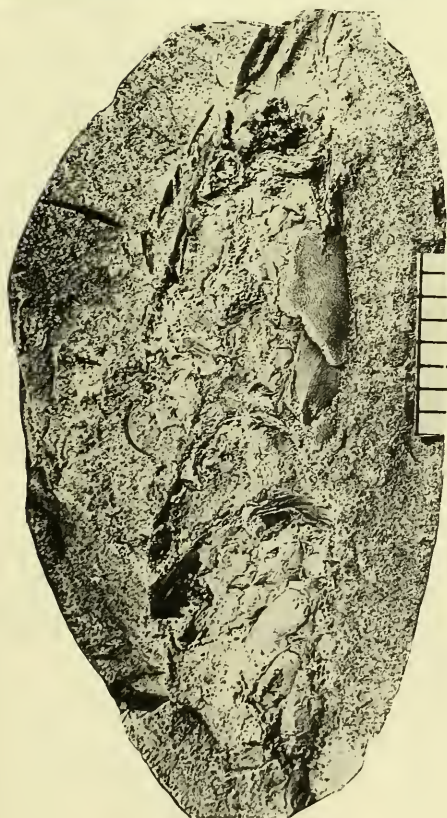
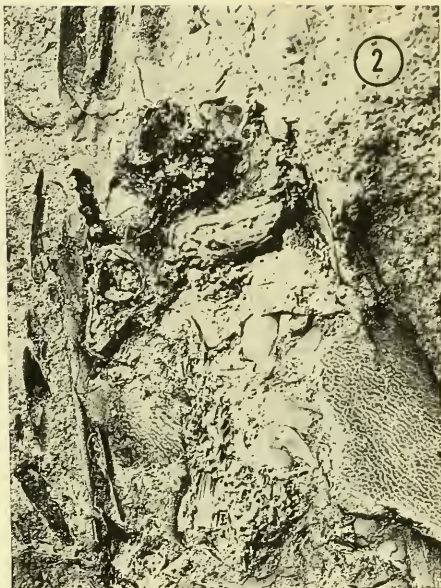
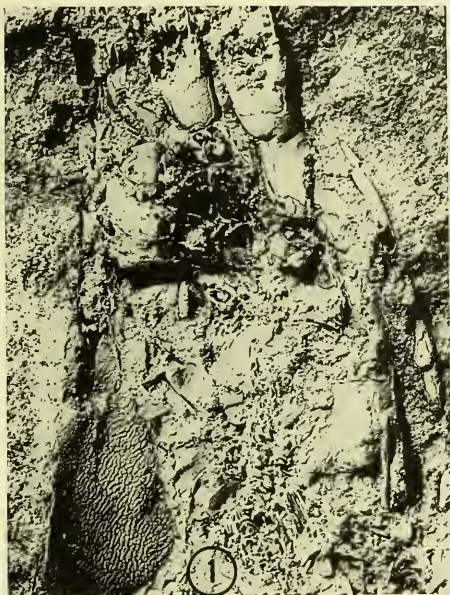


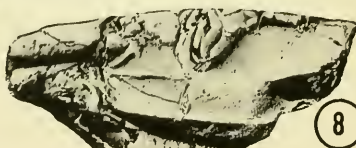
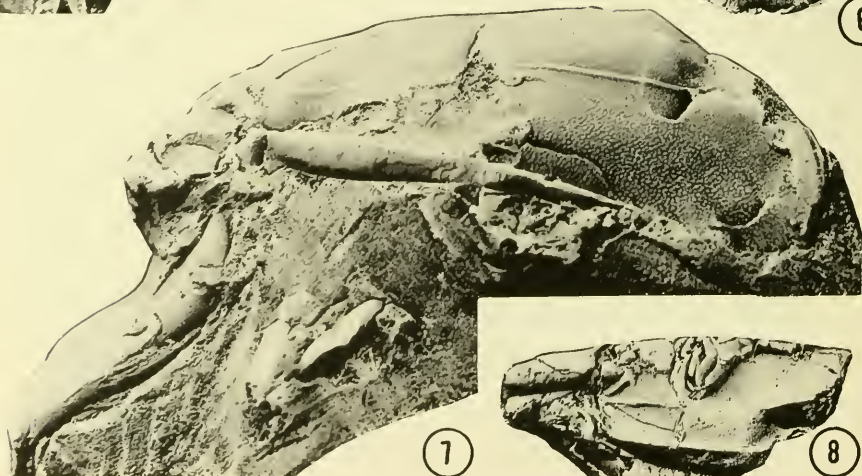
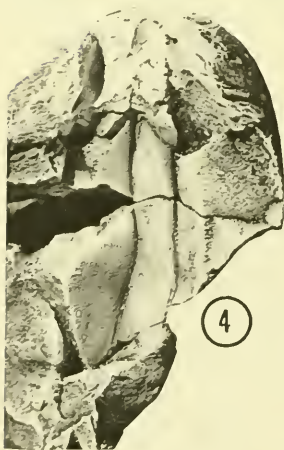
Explanation of Plate 48

| Figure | Page |
|--|------|
| 1. Anthracophausia strongi , n. sp. | 203 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 18821, holotype, X 4. | |
| 2. Counterpart of holotype, X 4. | |
| 3. Anthracophausia strongi | 203 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 18884, paratype, X 4. | |

Explanation of Plate 49

| Figure | Page |
|--|------|
| 1. Palaeopalaemon newberryi Whitfield New Providence fm., Lower Mississippian, Junction City, Ky., MCZ 5880, X 4. | 221 |
| 2. Counterpart, X 4. | |
| 3. Same specimen, X 2, stereograph. | |



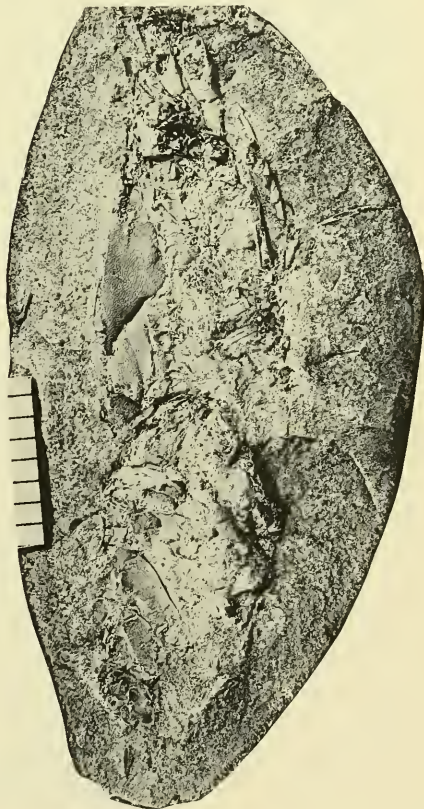
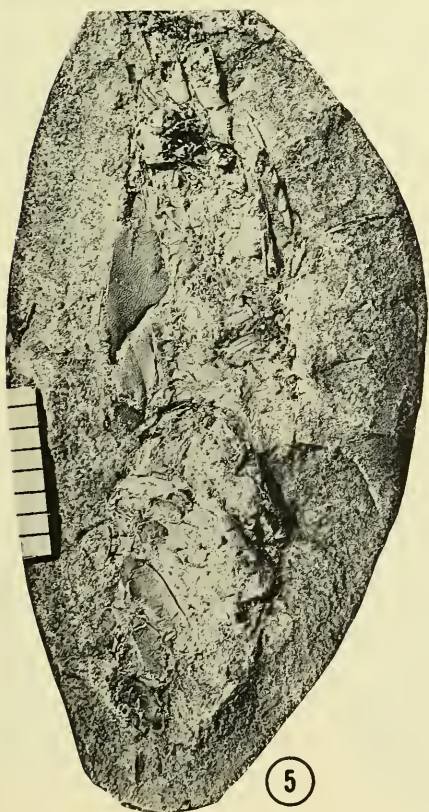
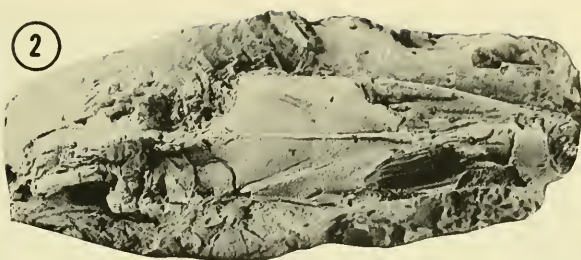


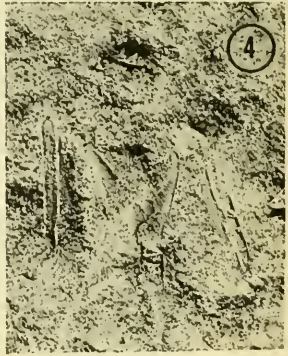
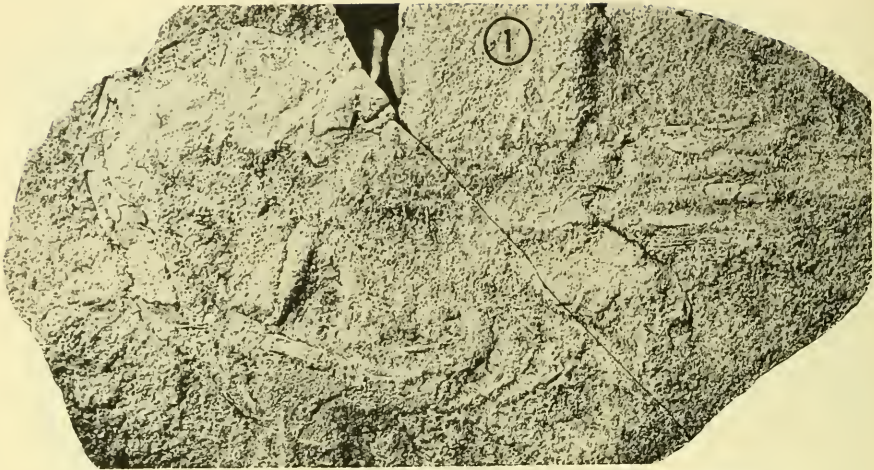
Explanation of Plate 50

| Figure | Page |
|---|------|
| 1. Palaeopalaemon newberryi Whitfield | 221 |
| Chagrin shale, Devonian, Painesville, Lake Co., Ohio, MCZ 6563, X 2. | |
| 2. Palaeopalaemon newberryi | 221 |
| Chagrin shale, Devonian, Leroy, Lake Co., Ohio, CU 6174, syntype (posterior of carapace and two abdominal tergites), X 5. | |
| 3. Palaeopalaemon newberryi | 221 |
| Chagrin shale, Devonian, Leroy, Lake Co., Ohio, CU 6714, syntype (caudal fan), X 6. | |
| 4. Palaeopalaemon newberryi | 221 |
| Chagrin shale, Devonian, Leroy, Lake Co., Ohio, CU 5514, syntype (carapace), X 2. | |
| 5. Palaeopalaemon newberryi | 221 |
| Chagrin shale, Devonian, Stebbins Gulch, Lake Co., Ohio, C1MNH 7628, dorsal view of carapace and pair of large basal joints of first antennae, X 3. | |
| 6. Rubber cast of CU 6714 (fig 3), X 5. | |
| 7. Palaeopalaemon newberryi | 221 |
| Chagrin shale, Devonian, Stebbins Gulch, Lake Co., Ohio, C1MNH 7628, lateral view of carapace and basal joint of first antennae, X 6. | |
| 8. Palaeopalaemon newberryi | 221 |
| Chagrin shale, Devonian, Leroy, Lake Co., Ohio, CU 5514, rubber cast of syntype, X 2. | |

Explanation of Plate 51

| Figure | Page |
|--|-------|
| 1. Palaeopalaemon iowensis Walter | 225 |
| Kinderhook shale, Mississippian, Burlington, Iowa, MCZ, 5106, | 518 G |
| joint of sympod of first antenna and exopodal scale of second | |
| antennae, X 5. | |
| 2. Same specimen, dorsal view of carapace, X 2. | |
| 3. Same specimen, lateral view of carapace, X 2. | |
| 4. Same specimen, joint of pereopod, X 10. | |
| 5. Palaeopalaemon newberryi Whitfield | 221 |
| New Providence fm., Mississippian, Junction City, Ky., MCZ 5880, | |
| X 2, stereograph. | |



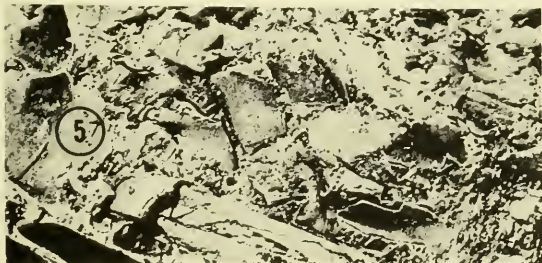
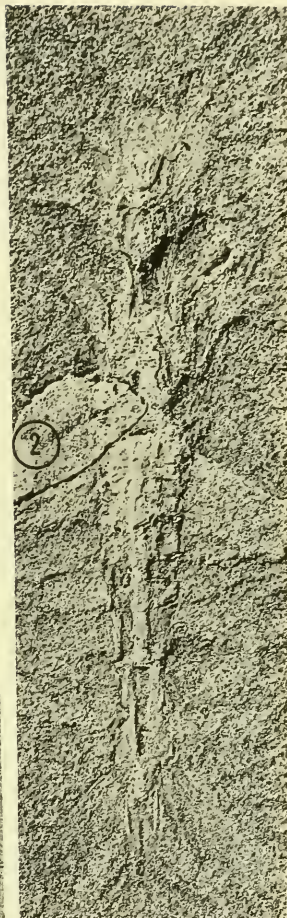
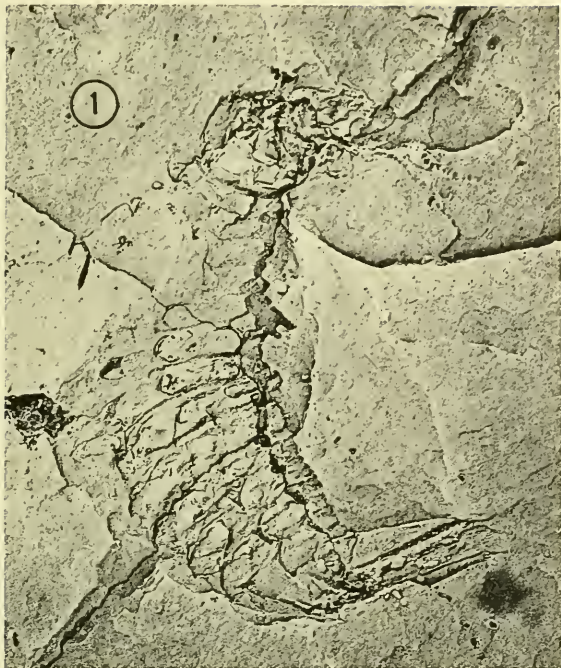


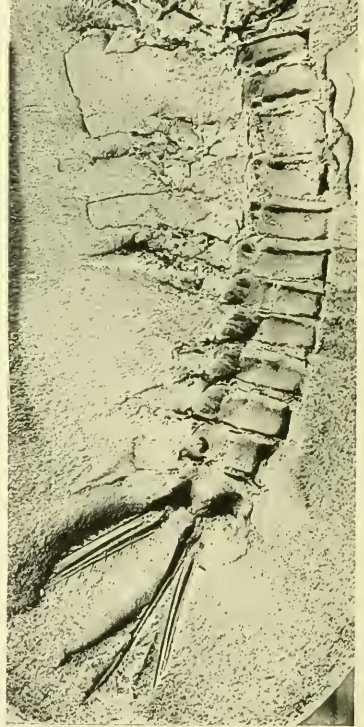
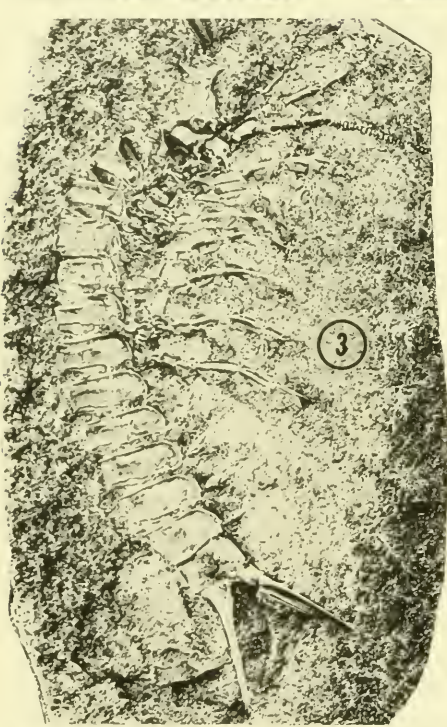
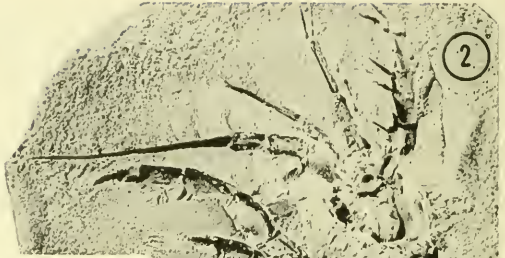
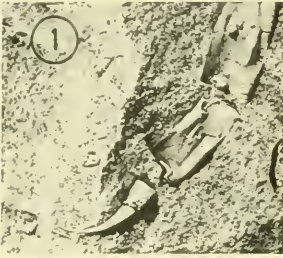
Explanation of Plate 52

| Figure | Page |
|---|------|
| 1. Belotelson magister Packard | 206 |
| Francis Creek shale, Pennsylvanian, Braidwood, Will Co., Ill., USNM 38844, Packard's (1886 a) plesiotype, X 1.5. | |
| 2. Belotelson magister | 206 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., USNM 38844, holotype, X 2.5. | |
| 3. Counterpart of holotype, X 1. | |
| 4. Remains of cephalic appendages on counterpart of holotype, X 2.5. | |

Explanation of Plate 53

| Figure | Page |
|--|------|
| 1. Squillites spinosus Scott Heath shale, Mississippian, Heath, Montana, UI X-1219, holotype, X 10. | 254 |
| 2. Devonocaris cuylensis (Wells) Moscow fm., Devonian, DeRuyter, New York, Cornell Univ. 40020, X 8. | 227 |
| 3. Squillites spinosus UI X-1219, counterpart of holotype, X 10. | 254 |
| 4. Devonocaris cuylensis Telson of holotype, X 15. | 227 |
| 5. Archaeocaris vermiformis Meek New Providence fm., Mississippian, Linietta Springs, PU 1597 d/5, sympods of thoracic appendages X 10. | 211 |



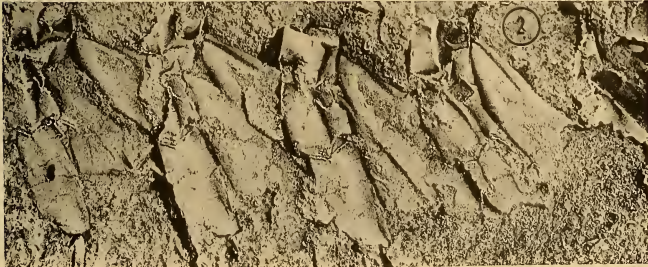
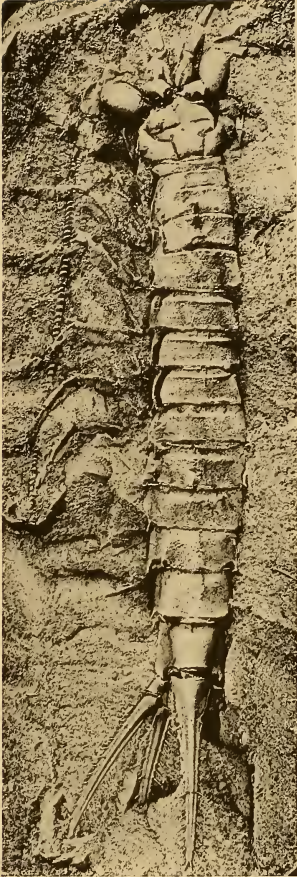
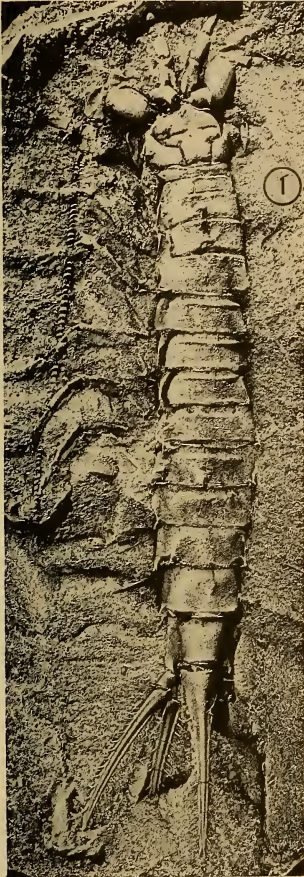


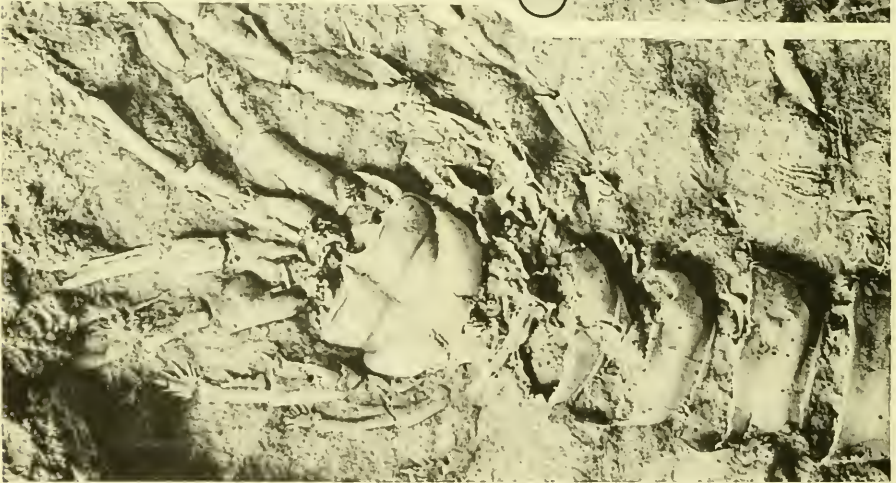
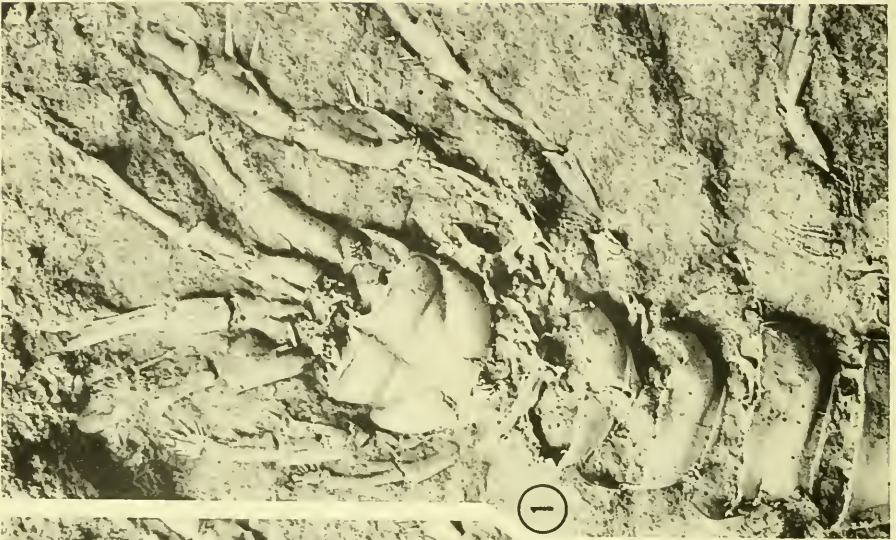
Explanation of Plate 54

| Figure | Page |
|--|------|
| 1. Acanthotelson stimpsoni Meek and Worthen Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19844, distal joints of raptorial appendage, X 5. | 230 |
| 2. Acanthotelson stimpsoni Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., USNM 38845, plesiotype of Packard (1886 a, pl. 2, fig. 1), X 2.5. | 230 |
| 3. Acanthotelson stimpsoni Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19867, X 3. | 230 |
| 4. Acanthotelson stimpsoni Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., UI X-346 (ISMNH 1118), holotype, X 3. | 230 |

Explanation of Plate 55

| Figure | Page |
|---|------|
| 1. Acanthotelson stimpsoni Meek and Worthen | 230 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., MCZ 5210, rubber cast, X 5, stereograph. | |
| 2. Acanthotelson stimpsoni | 230 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19640, rubber cast of epipods and exopods, X 10. | |



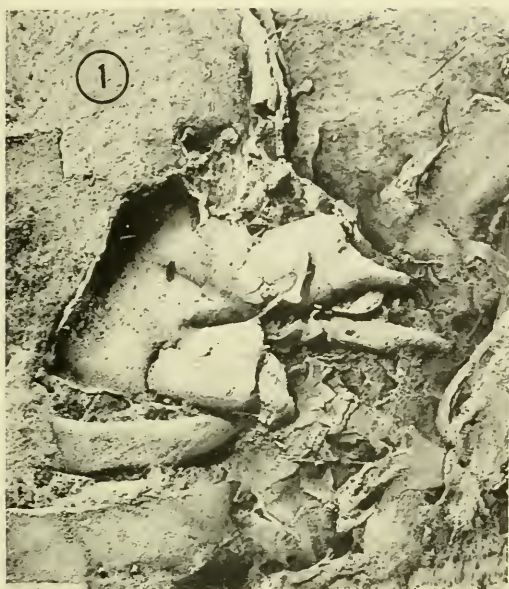


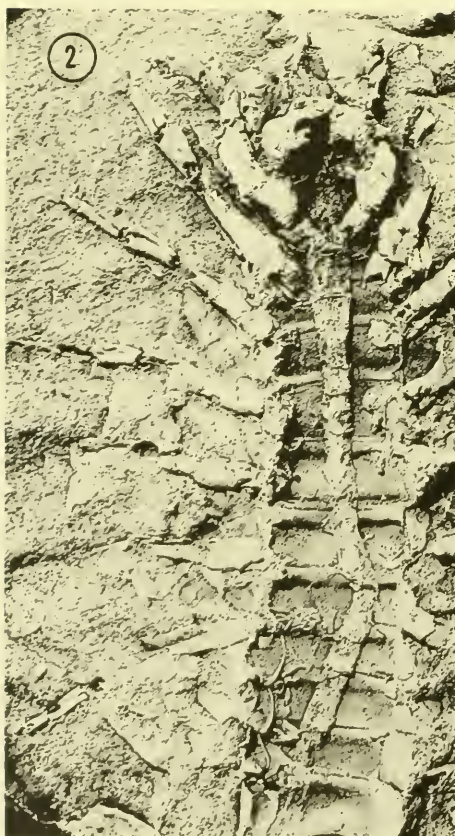
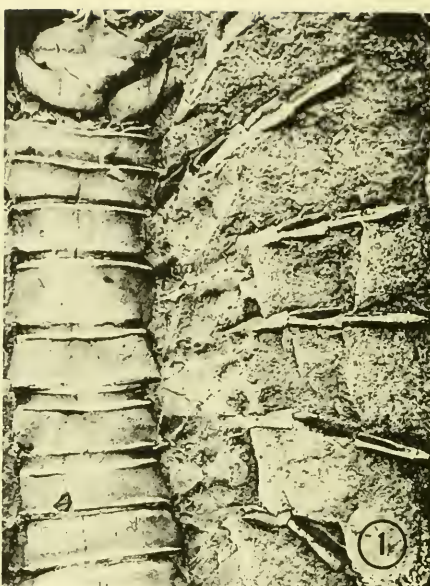
Explanation of Plate 56

| Figure | Page |
|--|------|
| 1. Acanthotelson stimpsoni Meek and Worthen | 230 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19842, rubber cast, X 5, stereograph. | |
| 2. Posterior of same specimen, rubber cast, X 5. | |

Explanation of Plate 57

| Figure | Page |
|---|------|
| 1. Acanthotelson stimpsoni Meek and Worthen Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19839, rubber cast of head showing mandible, paragnath and first maxilla, X 10. | 230 |
| 2. Counterpart of same specimen, rubber cast showing condyle of mandible, X 10. | |
| 3. Acanthotelson stimpsoni Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19902, X 5, stereograph. | 230 |



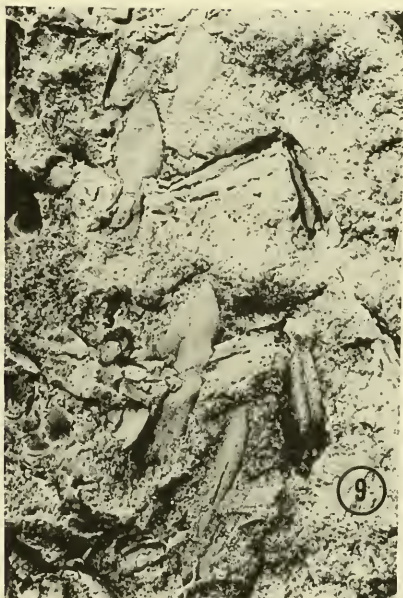
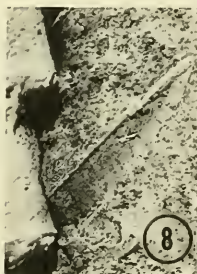
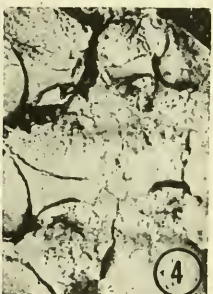
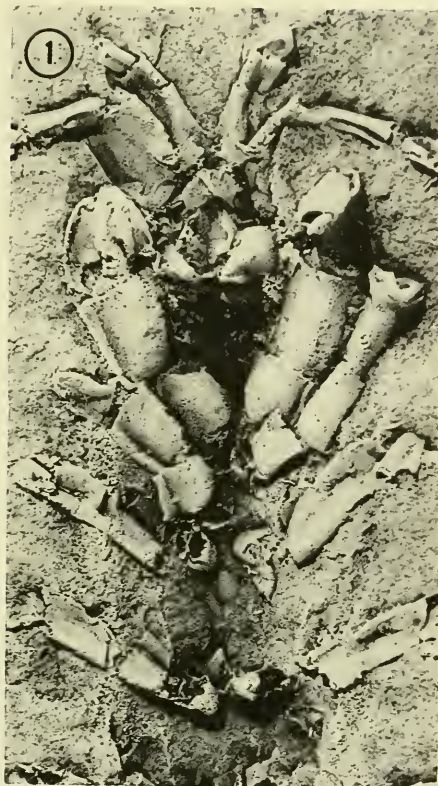


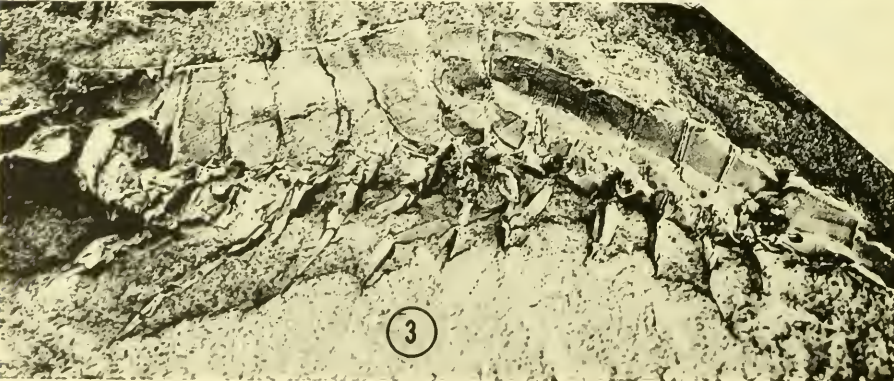
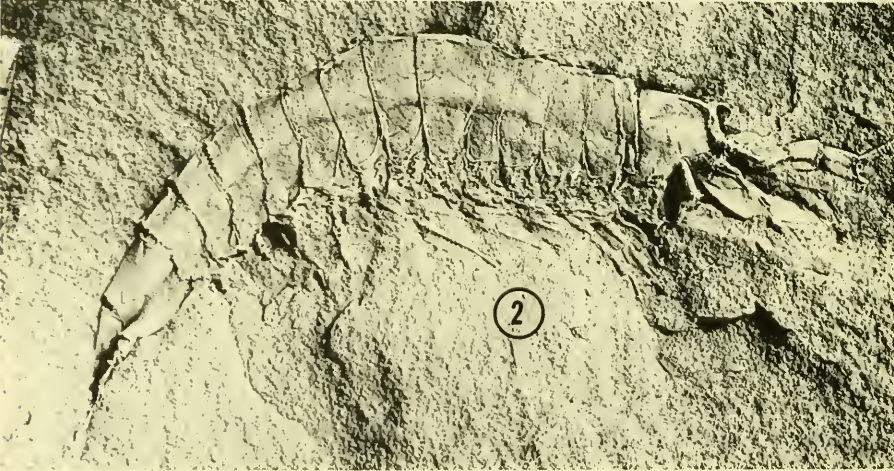
Explanation of Plate 58

| Figure | Page |
|---|------|
| 1. Acanthotelson stimsoni Meek and Worthen Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19744, rubber cast, X 5, stereograph. | 230 |
| 2. Counterpart of same specimen, rubber cast, X 5. | |
| 3. Acanthotelson stimpsoni Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19707, rubber cast showing sympods of thoracic appendages, X 10. | 230 |

Explanation of Plate 59

| Figure | Page |
|---|------|
| 1. Acanthotelson stimpsoni , Meek and Worthen | 230 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19854, rubber cast, X 10. | |
| 2. Acanthotelson stimpsoni | 230 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19653, rubber cast showing remains of first thoracic appendage, X 10. | |
| 3. Acanthotelson stimpsoni | 230 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19847, rubber cast showing thoracic sternites, X 10. | |
| 4. Acanthotelson stimpsoni | 230 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19817, abdominal sternites, X 6. | |
| 5. Acanthotelson stimpsoni | 230 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19707, rubber cast showing terminal joints of pereopods, X 10. | |
| 6. Acanthotelson stimpsoni | 230 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19867, rubber cast showing mandible and sympod of second antenna (note nephropore), X 20. | |
| 7. Acanthotelson stimpsoni | 230 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., MCZ 5224, rubber cast of dactylus of second thoracic endopod, X 10. | |
| 8. Acanthotelson stimpsoni | 230 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19846, rubber cast of exopod of pleopod, X 10. | |
| 9. Acanthotelson stimpsoni | 230 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19884, rubber cast of epipods and exopods, X 6. | |



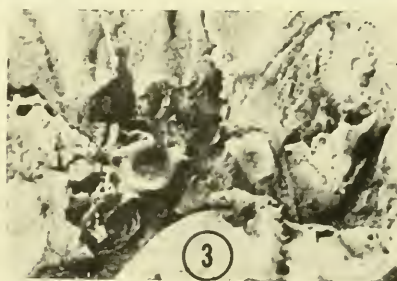
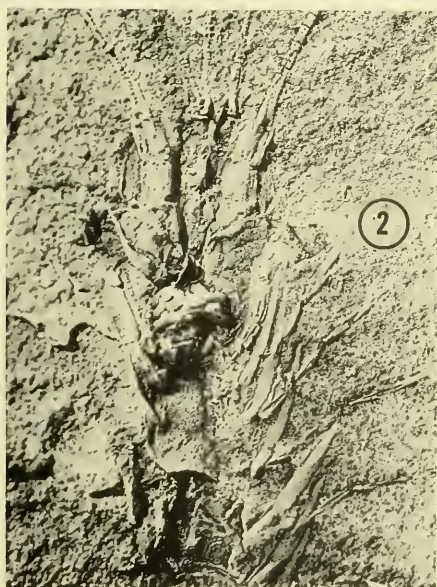
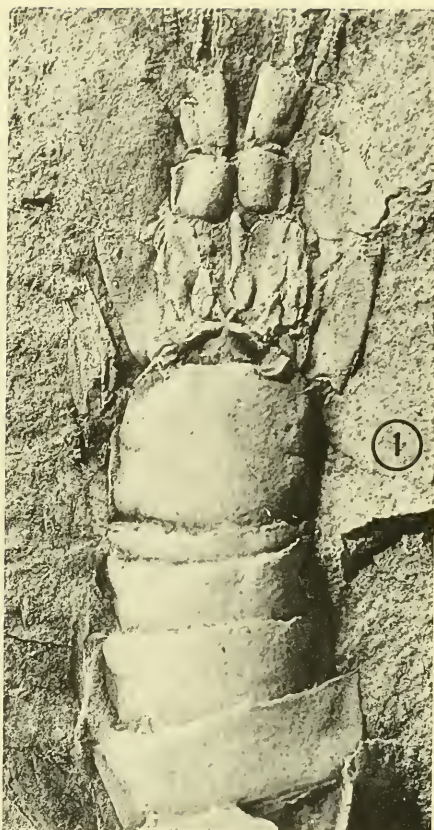
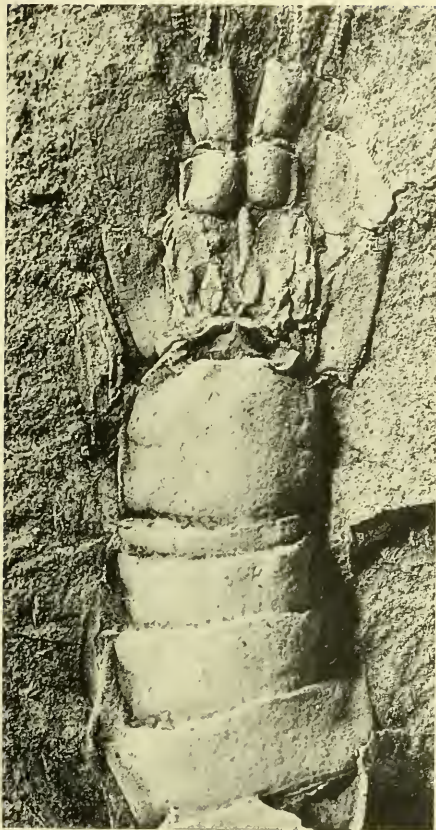


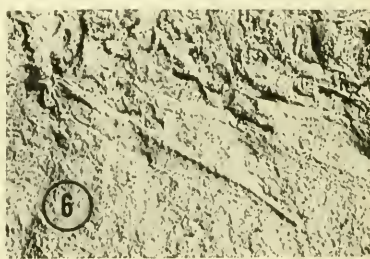
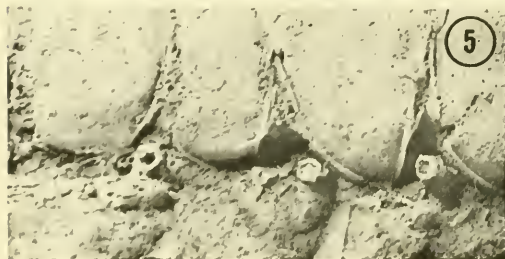
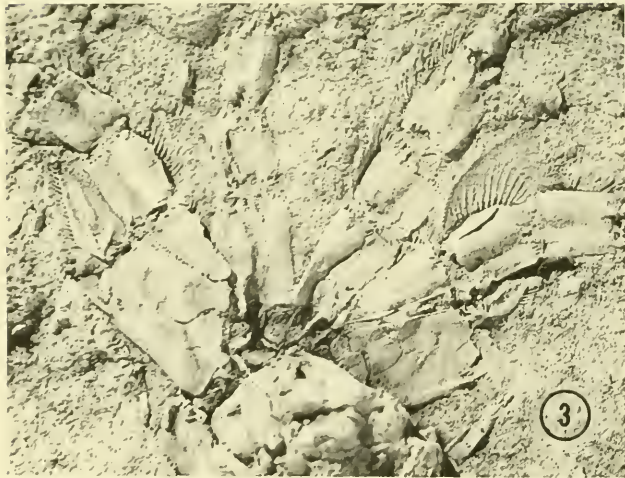
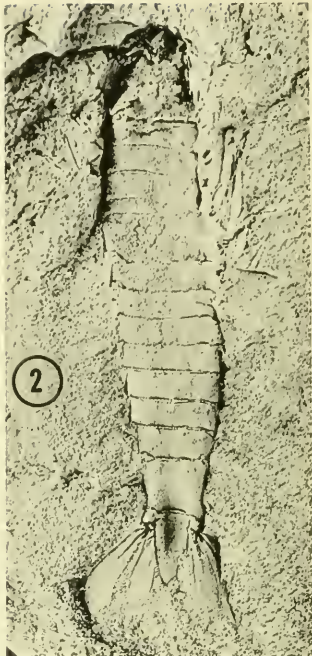
Explanation of Plate 60

| Figure | Page |
|---|------|
| 1. Palaeocaris typus Meek and Worthen | 240 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19755, rubber cast, X 4.5. | |
| 2. Palaeocaris typus | 240 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., MCZ 5197, rubber cast, X 6. | |
| 3. Palaeocaris typus | 240 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19750, rubber cast, X 5. | |

Explanation of Plate 61

| Figure | Page |
|---|------|
| 1. Palaeocaris typus Meek and Worthen | 240 |
| Francis Creek shale, Pennsylvanian, Braidwood, Will Co., Ill., CMNH 29405, rubber cast, X 10, stereograph. | |
| 2. Palaeocaris typus | 240 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19786, rubber cast, X 5. | |
| 3. Palaeocaris typus | 240 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19775, rubber cast showing epistome and basal joint of mandibular palp, X 20. | |
| 4. Palaeocaris typus | 240 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19812, rubber cast of labrum and second joint of mandibular palp, X 10. | |



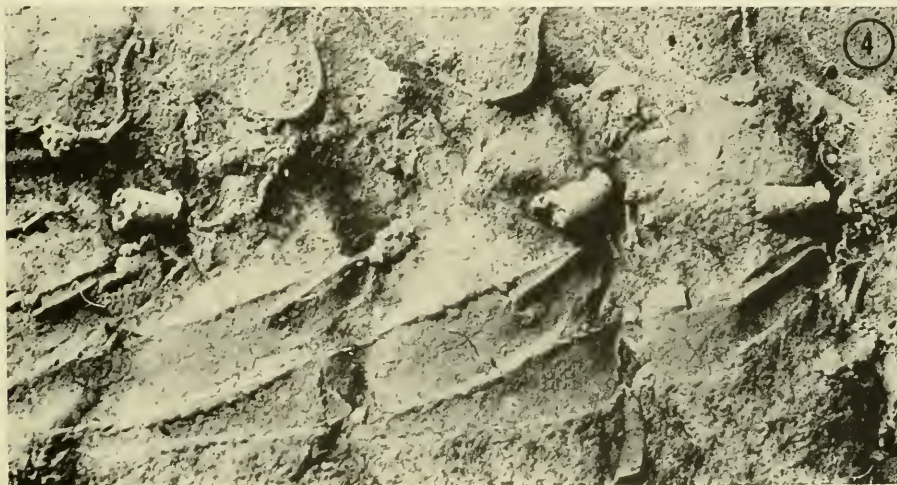
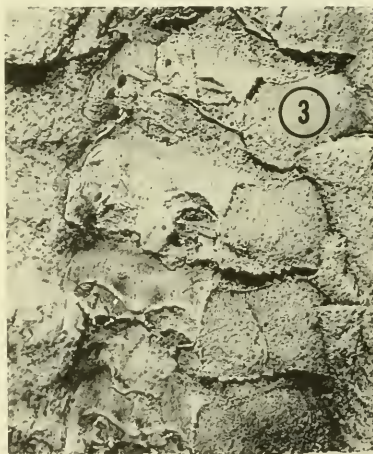
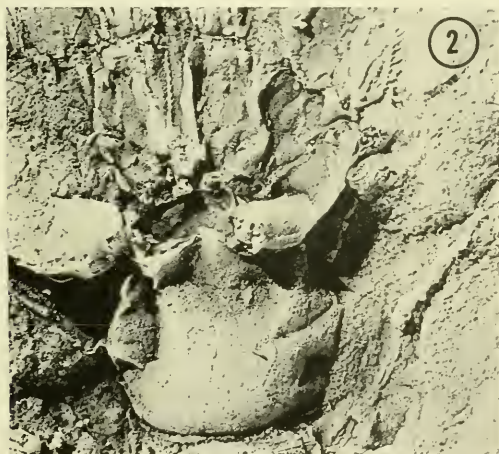


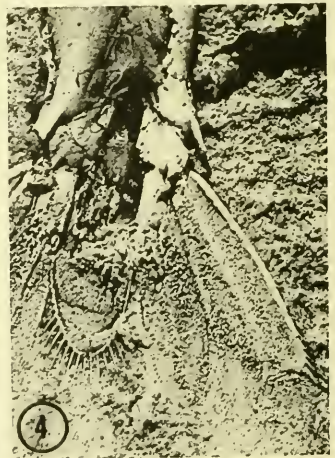
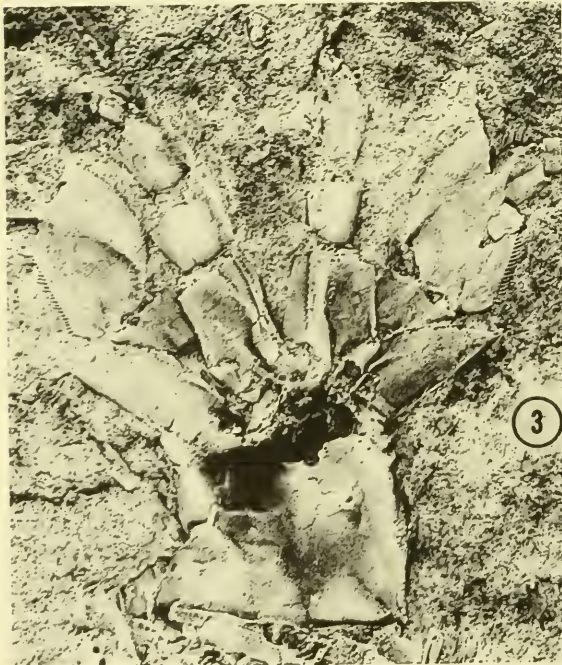
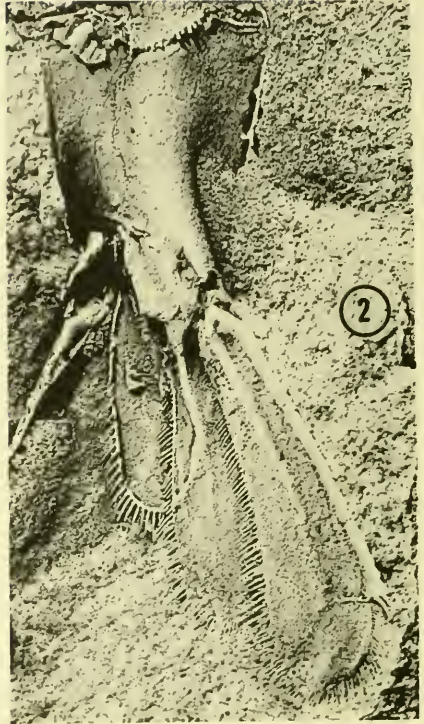
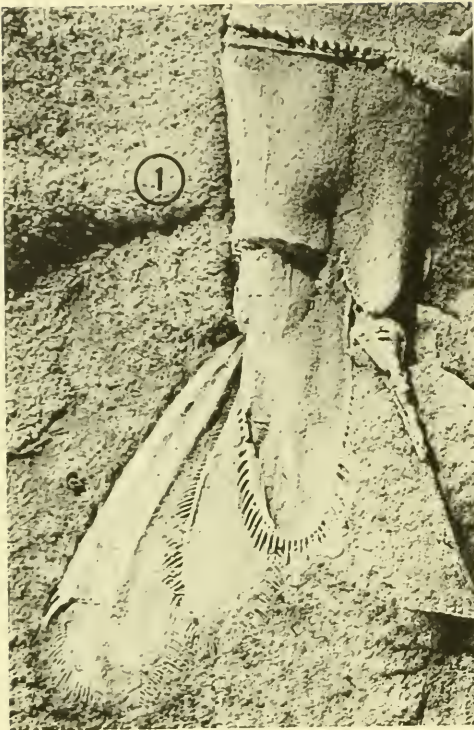
Explanation of Plate 62

| Figure | Page |
|--|------|
| 1. Palaeocaris typus Meek and Worthen | 240 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., USNM 38851, rubber cast of ventral structures of head, X 20. | |
| 2. Palaeocaris typus | 240 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., USNM 38850, plesiotype of Packard (1886 b, pl. 8, fig. 2), X 3. | |
| 3. Palaeocaris typus | 240 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19783, rubber cast of basal portion of antennae, X 10. | |
| 4. Palaeocaris typus | 240 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19755, rubber cast of anterior portion of fossil showing mandible, first and second maxillae, first thoracic endopod and an exopod, X 10. | |
| 5. Palaeocaris typus | 240 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19781, rubber cast of thoracic pleurae and bases of the epipods, X 20. | |
| 6. Palaeocaris typus | 240 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., MCZ 5197, rubber cast of exopods, X 10. | |

Explanation of Plate 63

| Figure | Page |
|--|------|
| 1. Palaeocaris typus Meek and Worthen | 240 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19731, rubber cast, X 4. | |
| 2. Palaeocaris typus | 240 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19823, rubber cast of dorsal features of head (note stalked eyes), X 10. | |
| 3. Palaeocaris typus | 240 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., USNM 38851, rubber cast of abdominal sternites, X 10. | |
| 4. Palaeocaris typus | 240 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19765, rubber cast showing epipods and exopods, X 10. | |



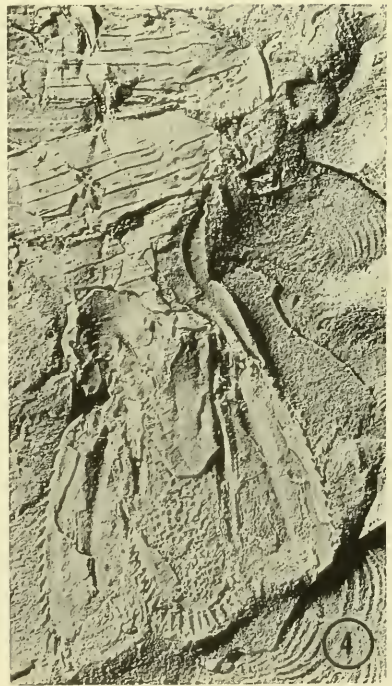
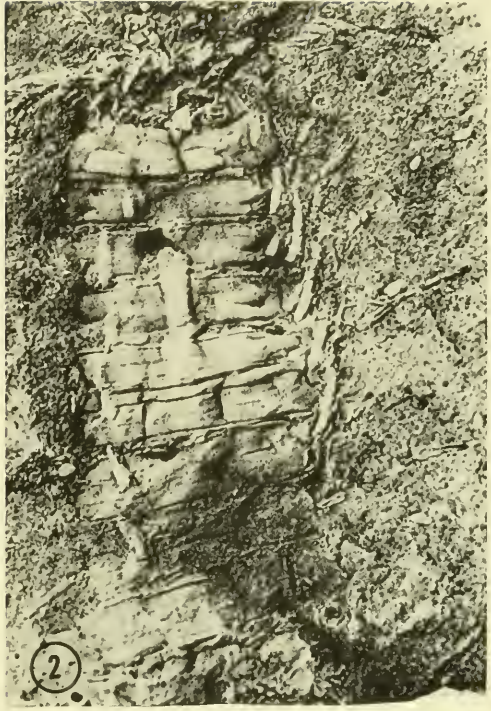
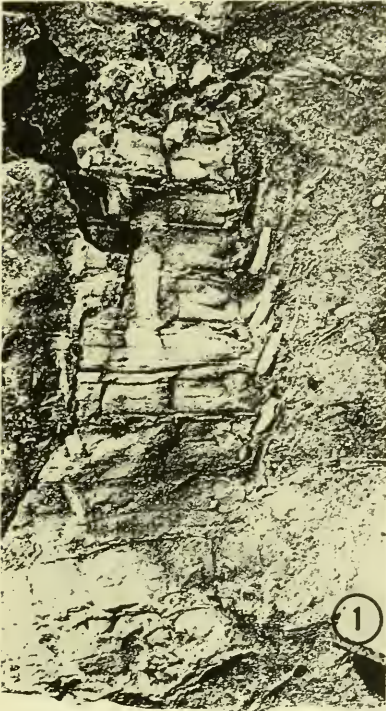


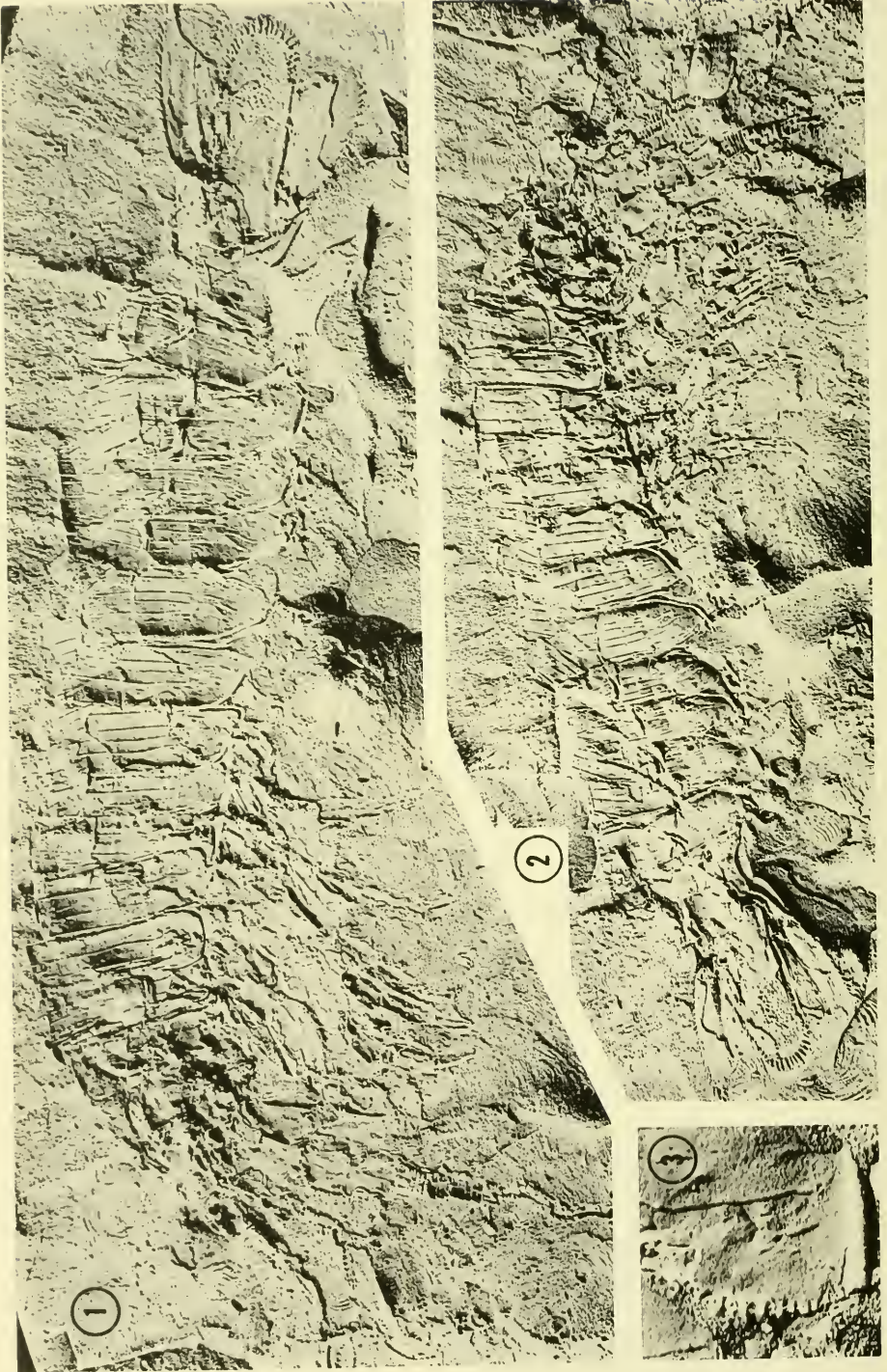
Explanation of Plate 64

| Figure | Page |
|--|------|
| 1. Palaeocaris typus Meek and Worthen | 240 |
| Francis Creek shale, Pennsylvanian, Braidwood, Will Co., Ill., CMNH PE-2511, rubber cast of sixth abdominal somite and caudal fan, X 10. | |
| 2. Counterpart of same specimen, X 10. | |
| 3. Palaeocaris typus | 240 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19783, rubber cast of first and second antennae, X 10. | |
| 4. Palaeocaris typus | 240 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19729, rubber cast of sixth abdominal somite and caudal fan, X 5. | |
| 5. Palaeocaris typus | 240 |
| Francis Creek shale, Pennsylvanian, Mazon Creek, Grundy Co., Ill., PY 19823, rubber cast of eye stalk (note papilla), X 15. | |

Explanation of Plate 65

| Figure | Page |
|--|------|
| 1. Palaeocaris canadensis , n. sp. | 248 |
| Riversdale grp., Pennsylvanian, Diligent River, Nova Scotia, MCZ 5435, holotype, X 10. | |
| 2. Rubber cast of counterpart of holotype, X 11. | |
| 3. Palaeosyncaris dakotensis , n. g., n. sp. | 251 |
| Heath shale, Mississippian, Starke Co., N.D., USNM 143409, first and second antennae, X 20. | |
| 4. Caudal fan of counterpart, Univ. N.D., X 20. | |





Explanation of Plate 66

| Figure | Page |
|---|------|
| 1. Palaeosyncaris dakotensis , n. g., n. sp. Heath shale, Mississippian, Starke Co., N.D., USNM 143409, holotype, X 10. | 251 |
| 2. Counterpart of holotype, Univ N.D., X 9. | |
| 3. Fifth abdominal pleura of same specimen, X 20. | |

INDEX

| | | | |
|---------------------|--------------------------------------|---------------------|-----------------------|
| H | | New Providence | |
| Heath shale | 257 | formation | 214, 224 |
| hillianus, | | Notocaris | 189, 265, 273 |
| Anthrapalaemon | 194 | novascotica, | |
| Horthon group | 219 | Acadiocaris | 217 |
| I | | O | |
| inaequalis, | | oervigi, Eocaris | 172, 260, 265 |
| Acanthotelson | 231 | Ohio shale | 224 |
| iowensis, | | Opeche formation | 188 |
| Palaeopalaemon | 51 225 | Oxyuropoda | 269 |
| Isopods, Paleozoic | 269 | | |
| Mesozoic | 270 | | |
| J | | P | |
| jepсени, | | Palaeocaris | 240, 262, 267, 273 |
| Mamayocaris | 44,45 189 | Palaeocrangon | 269 |
| K | | Paleoecology | 260 |
| Kinderhook shale | 226 | Palaeopalaemon | 219, 259, 265, 271 |
| Koonungidae | 274 | Palaeostomatopoda | 266, 272 |
| L | | Palaemysis | 272 |
| Leptostraca | 164, 168 | Palaeosyncaris | 250, 273 |
| Limulus | 259 | Pancardia | 268 |
| Liocaris | 189, 192 | Palaeopemphix | 269, 274 |
| M | | paradoxus, | |
| magister, | | Amphipeltus | 198,257, 269 |
| Belotelson | 52 206 | Paulocaris | 189 |
| Malcostraca | 163 | Peracarida | 268, 270, 273 |
| Mamayocaris | 188, 265, 272 | Perimecturus | 210, 263, 266, 272 |
| Mazon Creek nodules | 164, 188, 206, 210, 239, 248, 272 | Pennsylvanian | |
| Mississippian | | Eumalacostraca | 261 |
| Eumalacostraca | 260 | Permian | |
| Morphological | | Eumalacostraca | 262 |
| terminology | 167 | Permo-Triassic | |
| Moscow formation | 229 | Eumalacostraca | 269 |
| Mysidacea | 264, 265 | Phyllocarida | 163 |
| N | | Phyllogeny | 264 |
| Necrogammarus | 269 | Pictou group | 199, 250 |
| Necrosquilla | 193 | Pleurocaris | 274 |
| newberryi, Palaeo- | | Praeanaspides | 250, 251 |
| palaemon | 49-51 221 | Prearcturus | 269 |
| | | Preparation | 164 |
| | | Preservation | 174 |
| | | pruvosti, Eileticus | 258 |
| | | Pseudoteallicaris | 199, 265, 272 |
| | | Pygaspis | 189, 192 |
| | | Pygocephalus | 193, 265, 272 |
| | | Pygocephalomorpha | 265, 272 |

INDEX

| R | | T | |
|----------------------|--------------------|-----------------------|---------------------|
| Recapitulation, | | Tagmosis | 167 |
| embryological | 168, 243 | Tanaidacea | 268 |
| Riversdale group | 199, 250 | Tealliocaris | 199, 272 |
| S | | Terminology | 167 |
| Schimperella | 269 | Thermosbaenacea | 268 |
| socialis, Crangopsis | 205 | typus, | |
| Spelaeogriphacea | 268 | Palaeocaris | 60-64 240 |
| spinosus, Squillites | 53 254 | | |
| Squillites | 172, 229, 254, 273 | U | |
| Statistical analysis | 175, 262 | Uronectes | 230, 273 |
| stimpsoni, | | | |
| Acanthotelson | 54-59 230 | V | |
| Stomatopoda | 210, 263, 266 | Vale formation | 192 |
| Stratigraphic | | vermiformis, Archaeo- | |
| occurrence | 258 | caris | 45,46,53 211 |
| strongi, Anthra- | | | |
| cophausia | 48 203 | | |
| Syncarida | 229, 266, 273 | | |