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Malacostracan Crustacea from the Sundance Formation (Jurassic) of Wyoming

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Malacostracan Crustacea from the Sundance Formation (Jurassic) of Wyoming

(TITLE)

BY

Elizabeth M. Herrick

THESIS

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Taxonomy: Decapoda, Creustacea

Superfamily Penacidea Bate
Family Penaeidae Bate
Superfamily Eucyphidea Bate (= Caridea)
Family Uncinidae Beurlen
Family Udorellidae van Straelen
Family Atyidae Kingsley
Family Palaemonidae Bate
Superfamily Glypheidea van Straelen
Family Glyphaeidae Winkler
*Superfamily Paranephropsidea Beurlen
Family Erymidae van Straelen
*Superfamily Eryonidae de Haan
Family Eryonidae Dana
Family Platychelidae
*Superfamily Nephropsidea Alcock
Family Nephropsidae Stebbing
Family Astacidae Hagen
Family Parastacidae
Family Austroastacidae
Superfamily Thalassinidea Dana
Family Callianassidae Bate
Family Axiidae Bate
Superfamily Paguridea de Haan
Family Paguridae Dana
Superfamily Scyllaridea Borradaile
Family Palinuridae White
Family Scyllaridae White
Superfamily Galatheidea Leach
Family Galatheidae Dana
Family Porcellanidae Henderson
Family Albuneidae Stimpson
Superfamily Brachyuridea van Straelen (= Dromiacea de Haan)
Family Homolodromiidae Alcock

Superfamily Brachyuridea cont'd.

Family Prosoponidae v. Meyer
Family Dynomenidae Ortmann
Family Iatreillidae Alcock
Family Dakoticancridae Rathbun
Family Dromiidae Alcock
Family Cymopoliidae Faxon
Family Calappidae Alcock
Family Dorippidae Dana
Family Raninidae Dana
Family Portunidae Dana
Family Xanthidae Alcock
Family Ocypodidae
Family Leucosiidae Dana
Family Majidae Alcock
Family Parthenopidae Alcock
Family Atellecyclidae Ortmann
Family Cancridae Ortmann
Family Necronectidae Glaessner
Family Potamonidae Ortmann
Family Goneplacidae Dana
Family Pinnotheridae Milne-Edwards
Family Grapsidae Dana
Family Gecarcinidae Dana
Family Ocypodidae Ortmann

*In the Treatise, these superfamilies are grouped together under the Astacidea. The term Infraorder is substituted for the term Superfamily; Forster uses the term Division.

I. Introduction

Around 1810, three workers, two in France (Georges Cuvier and Alexandre Brongiart) and one in England (William Smith), published geologic maps that marked a great step foreward in the development of geology as a science[1]. People began to take a serious interest in fossils which had up to that time merely been looked at as curiosties. Studies of fossil decapod crustaceans began in earnest in the 1830's and since that time a vast store of information has accumulated. The fossil record presents some problems in the interpretation of the data by its very nature, and the situation is further complicated by some of the techniques used by early workers in the field. In the following analysis, keeping in mind these problems, we will focus our attention upon decapods preserved as fossils in the Mesozoic Era for the most part.

When one takes a look at the literature dealing with Mesozoic decapods it becomes readily apparent that most of the work has been concentrated in a few areas, primarily in Western Europe. Some work has been done on the African continent and parts of Central Asia, as well as in the United States. We have very little information from Australia, India, Russia, and almost nothing from South America. This paucity of

[1] Gilluly, J., A.C. Waters, and A.O. Woodford; Principles of Geology, 3rd ed., W.H. Freeman and Co.; 1968, p. 89.

data may be due to lack of interest, or unavailability of material for study, although the latter seems unlikely in many instances. The most thoroughly studied regions are in Germany, France, and England.

This spottiness of study areas introduces a certain degree of bias into a fossil record already beset by a number of natural factors that tend to distort the picture. These factors include environmental conditions unsuitable for preservation, metamorphosis and other forms of physical distortions of lithified sediments, erosion and subsequent reworking of rock units, general inaccessiblity of portions of the rock column, and a host of others[2]. The human element enters in again in the handling of data collected in the field. In general, early workers tended to classify variants as new species, and in many instances based their classifications on the most fragmentary evidentce, oftentimes describing an animal using a single chela or a small portion of carapace[3]. All of these forms of bias notwithstanding, we might perhaps note some trends in the decapod fossil record during the Mesozoic.

A number of superfamilies have no representatives in the Triassic at all, and most others are but poorly represented. Of those superfamilies with records in the Triassic, four are already well established in terms of numbers of species at the Permo-Triassic boundary and continue to be represented throughout the course of the Triassic. These groups

[2] See Raup, D.M. and S.M. Stanley, Principles of Paleontology; W.H. Freeman and Co., San Francisco; 1971, 37 Opp. for more complete coverage.

[3] See Berry, C.T., 1939. A summary of the fossil Crustacea of the order Stomatopoda, and a description of a new species from Angola. Amer. Midl. Nat., pp. 461-471, 2 figs. for a typical handling of data.

are all primitive, with a long, well developed abdomen, basically unspecialized pereiopods, and a subcylindrical carapace. By the beginning of the Jurassic, a trend toward increasing diversity on the species level can be detected, with several superfamilies making their first appearance at this time. A marked decline in all superfamilies can be noted during the early stages of the Cretaceous, with a general trend toward increasing numbers of species starting with the Albian, and reaching a climax during the Senonian. Most superfamilies are poorly represented in the Danian, the last stage of the Cretaceous.

In general, there seems to be a trend toward "carcinization" or "brachyurization", with extreme specialization of the pereiopods and the reduction of the abdomen with flexure, as evidenced by the porcellanids, the pagurids (possibly several times), the lithodids, culminating with the true crabs. The brachyurids are characterized by a carapace complete from top to bottom, carapace fused to all thoracic somites, and specialization of the pereiopods; the first is usually chelate and the first pair of pleopods in the male are modified for copulation. The first groups of decapods, and the most primitive, appeared at the Permo-Triassic and exploded during the Cretaceous. By the early Miocene the decapod fauna assemblage was essentially modern. Ninety percent of the genera were represented, and seventy per cent of the families contained conspecifics to modern forms.

II. Discussion

For the present study, the number of species belonging to each superfamily was used as a crude measure of diversity through time. A graph was set up with the geologic time scale running alsong the ordinate, and superfamilies along the abscissa, with numbers of species being plotted to facilitate comparison. (See figure 1. at the end for a general idea).

Two superfamilies, the Penacidea and the Glypheidea are present at the onset of the Triassic and are fairly well represented throughout (van Straelen and Schmitz, 1934; Förster, 1971; Pinna, 1967; Pinna, 1973). Penaeids are quite primitive: the carapace is laterally compressed and thin-walled, the rostrum is strong, the abdomen long, and the chelae of the first three pereiopods are similar in shape. The Glypheidea are not quite so primitive. The carapace is subcylindrical and slightly compressed laterally, the rostrum is small; the first three pereiopods do not have chelae.

Protoclytiopsis antiqua Birshtejn 1958, a nephropid, was originally described as being lower Triassic in age, but has since been moved down to the Permian (Birshtejn, 1958). Antrimpos madagascarensis Van Straelen 1936, appeared at the Permo-Triassic boundary (Förster, 1967), along with a number of paranephropsids (van Straelen and Schmitz, 1934), a relatively primitive group characterized by a subcylindrical cephalothorax, a well developed rostrum and abdomen, a pediform third maxilliped, and having the first three pereiopods chelate (of which the third is largest).

The superfamily Eryonidea has Permotrias representatives (van Straelen and Schmitz, 1934), and continues through the Triassic with

a rather sparse distribution (Schram, 1971; Pinna, 1969; Förster, 1967). The eryonids are characterized by a dorso-ventrally compressed carapace which is truncated anteriorly, pereiopods one through four or five chelate, and a long flat abdomen. This group is more specialized and advanced than the other groups considered so far. There have been reported six species of homarids, three each from the Skythian and the Carnian (Förster, 1967) including Clytiopsis argentoratensis and two unidentified species of the same genus from the former, and Clytiella spinifera, Paraclytiopsis hungaria, and Clytiopsis thuringica from the latter. The superfamily Caridea appeared late in the Triassic, with a single unidentified representative from the Norian (Pinna, 1973). These specimens could not be identified, according to the author, because the strata consisted of a coarse-grained limestone that had undergone considerable deformation.

Förster has suggested that the Pygocephalomorpha gave rise to the Palinura, the Brachyura, the Glypheocarida, and the Nephropsidea during the Triassic (Förster, 1967). Recent evidence indicates, however, that pygocephalomorphs were really peracarid mysids. They make their first appearance in the Pennsylvanian Essex fauna, at which time they were already quite specialized, with ancestors probably in the Devonian. More recent types apparently underwent convergent evolution. The Palaeopalaemonidae may be the first fossil decapods rather than the pygocephalomorphs. (see Schram, 1974 for a more complete discussion). Other groups of decapods are either poorly represented or have no record in the Triassic.

The beginning of the Jurassic saw a definite increase in diversity in all fossil groups except the Palinuridea and Homaridea for which we have no record for that time period at present. The Eryonidea, Penaeidea, and Glypheidea abruptly increased in numbers of species during the Rhaetian (van Straelen and Schmitz, 1934; van Straelen, 1925; Förster, 1973a). This is a rather advanced group with a carapace dorsoventrally more or less flattened, orbits in the anterior margin, and wide sternal plates.

The Nephropsidea got off to a slow start in the Jurassic with one species appearing in the Hettangian (van Straelen, 1925), and then radiating from the Pliensbachian through the Portlandian, reaching a peak in level of diversity at the close of the Jurassic (van Straelen and Schmitz, 1934; van Straelen, 1925).

The next three groups to be considered, the Paranephropsidea, Paguridea, and Eucyphidea show a similar pattern of development, with records beginning early in the Triassic, each superfamily being represented by only a few species. Radiations began in the Sinemurian for the paranephropsids and pagurids, and in the Toarcian for the Eucyphidea which have a poor record throughout most of the Jurassic but reach a peak in the Portlandian. The other two groups are well represented from the Sinemurian through the Portlandian (van Straelen and Schmitz, 1934; Neville and Berg, 1971). The Thalassinidea, Dromiadea, Galatheidea and Brachyuridea also show high levels of diversity with respect to numbers of species by the end of the Jurassic. These groups are represented by a few fossils until the Bajocian (van Straelen and Schmitz, 1934; van Straelen, 1925). Thalassinids are first found in the Pliens-

bachian (van Straelen, 1925), the Dromiadea next make their appearance in the Toarcian (van Straelen, 1925), followed by the galatheids and the brachyurids in the Bajocian (van Straelen and Schmitz, 1934). Each of these groups tend to undergo rather extensive radiations throughout the remainder of the Jurassic. The Thalassinidea are questionably anomurans; the Galatheidea and Paguridea are true Anomura, and ad such are highly specialized, being second only to the Brachyuridea or true crabs in complexity.

In general, then, the Jurassic seems to have been favorable for an increase in diversity, with nearly all groups undergoing radiations during the course of the Jurassic, reaching a peak during the Portlandian. Several superfamilies made their first appearance at this time, so that by the late Jurassic all major groups of decapod crustaceans are represented (van Straelen, 1925).

Förster indicates that interesting events were occurring with regard to the glypheids at this time. The genus Pseudoglyphea, which had undergone modification and consolidation during the Triassic, reached its maximum distribution during the earliest portion of the Jurassic, and apparently did not evolve further until its extinction in the Oxfordian. Mecochirus, probably an offshoot of Pseudoglyphea and more highly specialized, ranged from the Hettangian through the Campanian. It is inferred from fossil occurrances and associations that the Mecochiridae were shallow burrowers and carnivores, bearing a close relationship to Etallonia and Paleoaxius, the Jurassic ancestors of the recent burrowing group the Thalassinoidea (Förster, 1971). A thalassinid burrow

dating as far back as the Bathonian has been reported with Glyphaea undressieri (Meyer) remains inside the burrow from the Oxfordshire area in England (Sellwood, 1971). These Thalassinidea burrows are common trace fossils during the Jurassic (Förster, 1973b.), and give a further indication of the abundance of these forms.

Van Straelen states that decapods have been found in nearly all formations during the Jurassic, primarily in fine-grained sediments, and are especially abundant in formations with a neritic character. Typical Jurassic sediments include organic cozes, oolithic limestones, and lithographic limestones among others (van Straelen, 1925), sediments particularly favorable for good preservation of decapod remains. Examination of these sediments indicates that the Jurassic could be divided into two climatic zones, with several zoological provinces, including the "boreale russe, centrale-europeenne-mediterraneenne, indo-malaise-ethiopienne" (van Straelen, 1925). A colder climatic zone included the boreale russe province, and a warmer zone included the remaining two provinces. Although it is difficult to establish with certainty the fauna associated with each of these regions, it can be noted that Glyphea and Eryma appear frequently in both cold and warm zones, inferring that these two genera were eurythermal (van Straelen).

In contrast to the high levels of diversity that we find during the Jurassic, especially during the latter part, there is a definite decrease in the number of species per superfamily at the onset of the Cretaceous. There are progressively fewer records in the Valangian and Hauterivian, with no records at present for any superfamily during the Barremian. The

Eucyphidea have no record dating from the Valangian, but do reappear in the Coniacian (van Straelen and Schmitz, 1934). The Eryonidea are last represented in the Hauterivian (van Straelen and Schmitz, 1934). We have no record for the Penaeidea from the close of the Portlandian at which time they were one of the more diverse groups; they appear again in the Cenomanian. The peneids apparently did not radiate during the Cretaceous to the extent they had during the Jurassic (van Straelen and Schmitz, 1934). The Glypheidea (van Straelen and Schmitz, 1934; Förster, 1971), the Scyllaridea (Förster, 1973c; van Straelen and Schmitz, 1934), the Thalassinidea, the Galatheidea, and the Paranephropsidea (van Straelen and Schmitz, 1934) all show a pattern similar to that of the Penaeidea. The Nephropsidea and Brachyuridea, in contrast, are fairly well represented from the mid-Cretaceous, reaching relatively high levels of diversity by the Senonian (van Straelen and Schmitz, 1934; Förster, 1968; Jux, 1971; Förster, 1970a; Bishop, 1972).

According to Förster, the Brachyuridea were undergoing important changes during the Cretaceous, similar to the Jurassic glypheid radiations. Necrocarcinus is believed to be derived from the Jurassic Dynomenidean Cyphonotus oxythyreiforme (Gemellaro). Förster thinks that the Necrocarcininae might have given rise to the Xanthidae and Portunidae during the Cretaceous. A number of species were splitting off from major lines throughout the course of the Cretaceous with a number of forms going extinct, but others giving rise to new lines (Förster, 1968). In a later paper, Förster suggests that the Necrocarcininae and Raninidae shared a common ancestor early in the Cretaceous (Förster, 1970b). We might conclude, then, that a number of decapod superfamilies were already fairly

well differentiated at the close of the Jurassic, and did not change to an appreciable extent during the Cretaceous. The Nephropsidea and the Brachyuridea, on the other hand, did undergo extensive radiations throughout the latter part of the Cretaceous.

The above-mentioned trends seem to be fairly well established, but one might reconsider the bias problem at this point. Jurassic sediments were unusually well suited for the preservation of crustaceans, whereas it is likely that conditions in the Cretaceous were not quite so favorable. Sampling bias is nicely illustrated by the work of Bishop in the United States. This worker recorded over 4,000 specimens belonging to a single genus and species from the Pierre Shale of South Dakota (Bishop, 1972). Clearly the environment was capable of supporting large numbers of animals, but Mesozoic formations have been largely neglected in the United States, so that what data we do have comes primarily from a few study areas on Europe. Such forms of bias tend to limit an analysis to a rough outline of the events occurring over long periods of time in the past.

III. Summary

Several of the superfamilies under consideration were already fairly well represented at the Permotriassic boundary, including the Eryonidea, Penaeidea, Glypheidea, and Paranephropsidea. The Homaridea apparently made their first appearance during the Skythian; all groups underwent modification and consolidation during the Triassic, with no evidence of major radiations in any of the groups until the last of the Triassic.

The Jurassic saw the establishment of a nearly modern assemblage, with all major groups being represented by the turn of the era. It was during the Jurassic that the most extensive radiations occurred, notably in the Glypheidea and in the Brachyuridea. The latter group, along with the Scyllaridea, Thalassinidea, Dromiadea, Galatheidea, Palinuridea, and Paguridea all made their appearance at some point in the Jurassic, and they all increased in diversity reaching relatively high levels by the Portlandian.

During the Cretaceous, the only group to undergo major radiations were the Brachyuridea, continuing a trend established in the mid-Jurassic. The early portion of the Cretaceous is characterized by a decrease in diversity levels among all superfamilies. Few records have been brought to light for the mid-Cretaceous. There seems to be a trend toward increasing diversity by the late Cretaceous, but not to the extent reached by the late Jurassic.

It is important to keep in mind the fact that our knowledge of Mesozoic decapods is of a fragmentary nature when considering early radiations. Undoubtedly further study will improve our understanding of the events occurring in the distant past.

Abstract

The decapod fauna from the Stockade Beaver Member of the Sundance Formation of Wyoming is described. The Sundance Formation represents the only marine Jurassic deposits in North America. Preservation of the crustaceans in the Stockade Beaver Shale Member of the Sundance Formation is only moderately good, permitting identification at most to the generic level of these soft-shelled decapodous shrimps. The faunal assemblage, composed of *Antrimpos* sp., *Bombur* sp., *Mecochirus* sp., a glypheid, and some unidentifyable anomuran remains, can be compared to Triassic and Jurassic material from European deposits, and form part of a continuum throughout the Lower Mesozoic.

Introduction

Strata of marine Jurassic age are lacking for the most part in the United States, being known only from the Black Hills area and somewhat westward. The remainder of North America was subaerially exposed during the Jurassic and has no sediments of marine origin deposited (Gignoux, 1955). The Black Hills Jurassic formations were first described in detail by Darton (1899). We are concerned here only with the Crustacea of the Sundance Formation (Callovian-Oxfordian), with special emphasis on the Stockade Beaver Shale Member. The material was collected from the Stockade Beaver Member of the Sundance Formation from Bush Canyon, 2.5 miles north of Hulett in S25 and 36, T55N, R65W, Crook County, Wyoming.

The Sundance Formation consists of five members, and has a range of 200 to 350 ft. (75-115 m) in thickness. The Stockade Beaver Shale Member is bounded basally by the Canyon Springs Sandstone Member, and is overlain by the Hulett Sandstone Member, and averages 50 ft (15 m) in thickness, although it ranges from 5 to 85 ft (1.5-26 m) (Imlay, 1947). The Stockade Beaver Member is primarily a medium to dark gray, soft, fissile, calcareous shale. In the southern and central portions of the Black Hills fossils are fairly abundant and the sediments are quite calcareous. Northward fewer fossils are found, the sediments are less calcareous, and soft, greenish gray to yellowish gray siltatone and sandstone begin to appear. According to Imlay (1947), these sediments are a result of a marine transgression that covered a large area and deposited soft, gray, calcareous clastics originating from the south and southeast. The environment was lageonal, with a tropical or subtropical climate.

The Stockade Beaver Shale Member is significant because the environment of deposition was favorable for preservation of forms that were usually weathered during transport, before they could be buried. A number of soft-shelled, intact decapod shrimps have been found. The Stockade Beaver Shale is an important source of Jurassic decapod material in that it is the only known source in North America.

The following is a discussion of the fossil decapods found in the Stockade Beaver Shale. The specimens are preserved as carbonized remains with the cuticular structures relatively undistorted. In some instances portions of the integument were lost leaving only an imprint or mold of the cuticular structure. The material, while generally composed of

whole animals, is unfortunately not preserved well enough to allow identification to the species level. Nevertheless, this fauna forms an important contribution to the knowledge of Jurassic Malacostraca.

For the most part there were large numbers of individuals in a localized area, implying mass burial of these organisms. Four, possibly six species were preserved, but the genus Antrimpos was the dominant form in terms of numbers of individuals. The specimens were collected by Dr. Bobb Schaeffer, and are deposited in the American Museum of Natural History (AMNH).

Systematic Descriptions

Class Malacostraca Latreille, 1806

Subclass Eumalacostraca Grobben, 1892

Superorder Eucarida Calman, 1904

Order Decapoda Latreille, 1803

Suborder Dendrobranchiata Bate, 1888

Infraorder Penaeidea de Haan, 1849

Family Penaeidae Rafinesque, 1815

Genus Antrimpos Münster, 1839

Antrimpos sp. (Figs. 1a and 2d)

Description of specimens - 36244-36261, 36267, and 36269. The specimens were preserved as laterally compressed organic remains, that had undergone partial decomposition, and as distorted molds.

The carapace has a well developed ventrally curved rostrum with five or six dorsal teeth (36257a, 36245a, 36259a, Fig. 2d). The body

is laterally compressed and the carapace is thin and uncalcified with a marginal doublure (36247a). No grooves or other surface ornamentation were preserved. The pereiopods are long and slender; the merus seems to be slightly longer than each of the remaining segments, but poor preservation prevents actual measurement or absolute size comparisons. The first three pereiopods are chelate, and pereiopods 4 and 5 exceed the first three in length (36259a). There are no spines or any other ornamentation on the pereiopods. The scaphocerite is large and oval. No other details of the antennae are discernable.

The abdomen is well developed. Abdominal segments 1 through 5 are approximately equal in length, the sixth being longer than the others. The pleurite of the second somite does not overlap the first. The pleurites are rounded (36259). The telson is triangular and the uropods are leaf shaped without a diaresis (Figs. 1a, 2d). Only the proximal portion of the pleopods were preserved.

Remarks: Out of some 45 individuals, no one specimen was preserved in toto. The above description and reconstruction Fig. 1a is thus based on a composite. None of the specimens has a complete rostrum, although it is partially preserved on 36245a, 36257a, and 36259a. The posterior portion of the carapace showing the doublure in most cases has been obliterated. These animals were buried as whole organisms rather than as exuviae, since the carapace does not show any evidence of molt sutures. Nor is any specimen in the Salter position (Bishop, 1972), i.e. with carapace up at an angle of 45° with respect to the abdomen. The coxal and basal segments of the pereiopods are not visible, and the

pereiopods are not so well preserved as to be able to distinguish all segments; e.g. the joint between the dactylus and propodus cannot be seen. The scaphocerite, eye, and pleopods were usually incompletely preserved as molds.

These specimens were placed in the genus Antrimpos for the following reasons: The rostrum is ventrally curved and dorsally dentate, the carapace is thin and smooth, the first three pereiopods increase in length, are chelate, and without spines. The sixth abdominal somite is longer than the other five. The rostrum is the most important characteristic that separates these animals from other penaeids which have a dorsally curved rostrum or a simple, blunt rostrum. The first three chelate pereiopods without spines and the longer sixth abdominal somite serve to distinguish these animals from Aeger, Acanthochirana, and the remaining penaeids. Representative measurements are given in Table 1.

Genus Bombur Münster, 1839

Bombur sp. (Figs. 1d and 3a, b)

Description of specimens - 36257b, 36258, 36261a, and 36263. These specimens were small forms with a simple, short, blunt rostrum (36261a, Fig. 3a). The body is laterally compressed. The carapace is thin and uncalcified, and smooth. Pereiopods 4 and 5 are long and slender, and achelate. There are no discernable details for any of the other pereiopods (36263, Fig. 1d). Antennular details are lacking on all specimens. The eye stalk can be seen on 36261a, along with a preorbital spine.

The abdomen is well developed and bent. The pleurite of the second pleomere does not overlap the first, and the sixth somite is longer than the others. The uropods are small, and the pleopods are paddle shaped (36257b). The telson appears to be triangular (36261a, Fig. 3b).

Remarks: The cuticle of these animals was apparently very thin and did not preserve well. Two specimens (36257b and 36263) have lost large portions of the integument and are preserved only as molds. The pereiopods in most cases have not been preserved at all, although two appendages can be seen on 36263. They are taken to be pereiopods 4 and 5 based solely on their position with respect to the carapace, since coxa and basis were not preserved. The uropods do not seem to have been sclerotised and are folded against the telson, and thus were poorly preserved (36261a, 36263, Fig. 3a). There is no evidence of molt sutures, implying as in Antrimpos sp., burial of dead organisms rather than of exuviae.

These specimens were assigned to the genus Bombur because they have a simple, blunt rostrum; a thin, smooth carapace; and a flexed abdomen with the sixth somite longer than the first five. The cephalothorax is fairly short. The shape of the rostrum, the overall size of the animals, the character of the sixth abdominal somite, and the size of the cephalothorax serve to distinguish these organisms from the other penaeids.

Bombur has been heretofer poorly known. Glaessner (1969) states only that Bombur is a small form with a small rostrum, a short cephalothorax, a bent abdomen, and a long sixth somite. The sundance material gives some added insight into such anatomical features as the eye and the

anterior portion of the carapace including such details as the rostrum and the preorbital spine, along with some indication of the structure of some of the appendages, for example pereiopods 4 and 5 and the pleopods. Measurements are given in Table 1.

Infraorder Palinura Latreille, 1803

Superfamily Glypheoidea Winkler, 1883

Family Mecochiridae van Straelen, 1929

Genus Mecochirus Germar, 1827

Mecochirus sp. (Figs. 1e, 2a, and 2c)

Description of specimens - 36264A and B, and 36265. The carapace is subcylindrical and was very thin. Only the branchiocardaic and postcervical grooves were preserved and are partially visible. The first pereiopods are long and slender, and apparently subchelate (Fig. 2a and c). The first pereiopods of 36264 are approximately half the length of the body, measured from the base of the rostrum to the telson. The first pereiopods of 36265 are estimated to be 22 mm in length, compared with 28 mm for the length of the body. These figures give only a rough approximation, however, because the dactylus was broken off when the specimen was collected, and the coxa and basis were not preserved. The anterior of the carapace was also broken off, and the telson is buried in the matrix, so an exact body length could not be determined either. No other appendages can be seen on 36264.

The abdomen is long and well developed. Pleomeres 2 through 6 are subequal in length, and the first pleomere is slightly reduced. The uropods are fan shaped without a diaresis.

Remarks: The material available consists of two incomplete individuals (36264A and B, and 36265), and possibly a third very poorly preserved specimen (36266A and B). The anterior portion of the carapace was badly preserved and distorted, so these organisms cannot be assigned to a specific species. The subchelate nature of the first pereiopods is clearly illustrated on 36265 (Fig. 2a), although nothing can be said of the other thoracic appendages. No antennular details were preserved. The animal was preserved in life position (Fig. 2a and c), so abrupt burial of a live, reptant organism is implied.

The placement of these specimens in the genus Mecochirus was based on the following criteria: The long, slender, subchelate first pereiopods, and the smooth, thin carapace, along with the position of the branchiocardiac and postcervical grooves. The above characteristics serve to distinguish Mecochirus from its more heavily calcified relatives including Meyeria and Selenisca that also have a heavy first pereiopod. The first pereiopod of Pseudoglyphea are slightly more developed than those of Mecochirus and are spinose.

Family Glypheidae Winkler, 1883

Genus Uncertain (Figs. 1f, 3d)

Description of specimens - 36270 and 36271A and B. The carapace was well sclerotised and the body is subcylindrical. Only portions of the branchiocardiac and postcervical grooves were preserved. The first pereiopods are long, flattened, strongly calcified, and achelate. The dactylus cannot be distinguished from the propodus, nor are the coxa and basis visible on either specimen. The second pereiopod appears

to be subchelate, and the third is chelate (36270, Fig. 1f). The antennular flagellum is moderately long, approximately as long as the first pereiopod. Tubercles might be present on the anterior portion of the carapace, but preservation was poor and most of the details were obscured. No other ornamentation on the carapace or pereiopods was preserved.

The abdomen is not as well developed as in Antrimpos, Bombur, and Mecochirus. The first plenere did not preserve well, but seems to be slightly reduced. Pleura of the second abdominal somite are broadly rounded while the pleura of the third are less so. Specimen 36270 was preserved with the abdomen strongly flexed, so that little of the telson and uropods can be seen. Specimen 36271 was dorso-ventrally compressed, and the fan shaped uropods with a diaresis and broadly rounded telson can be seen (Fig. 4). The uropods are setose.

Remarks: The description is largely based on specimen 36270, although 36271, though more poorly preserved, is taken to represent a congeneric organism. The anterior portion of the carapace is obliterated, along with most of the more important diagnostic characteristics of the pereiopods, making it difficult to assign this animal to the generic level. None of the appendages were preserved on 36271. Although the first pereiopod of 36270 is clearly long and flattened, the carpus cannot be distinguished from the merus (similarly for the propodus and dactylus as noted above). Coxal and basal segments were not preserved on any of the pereiopods. The chelate nature of the third pereiopod can clearly be seen (Fig. 1f), but the distal portion of the second pereiopod was not well preserved and it is difficult to determine

whether the appendage is subchelate or chelate; however, it is clearly one of these two choices, as opposed to being achelate (Fig. 3d). These animals appear to be glypheoids, based on the flattened first periopod, the branchiocardiac and postcervical grooves, and the structure of the abdomen.

Unidentifiable Material

Description of specimens - 36267a and 36268a. Also included in the Stockade Beaver crustaceans are two fragments of heavily calcified decapod remains (36267a and 36268a). One fragment (36267a, Fig. 2b), seems to be part of a carapace that was badly weathered before burial. Prominent tubercles are present, randomly distributed over the entire surface.

The second fragment (36268a, Fig. 3c), seems to be part of a thoracopod manus. There is a raised central portion with diagonal furrows along the length of the fragment. Again, tubercles are present, but they appear to have a slightly more orderly arrangement tending to be arranged in bands parallel to the median grooves (Fig. 1c). The outer margin of the fragment gives the appearance of spines having been broken off (Fig. 1c). If 36268a is indeed part of a manus, then it represents yet another decapod than those previously considered, and of a more advanced type, because a heavily calcified and large thoracopod was only developed toward the end of the Jurassic and Cretaceous in groups such as the family Axiidae in the infraorder Anomura.

Discussion

A number of assorted pelecypods, a brachiopod, a belemnoid, and a crinoid among others have been described from the Stockade Beaver Member of the Sundance Formation (Imlay, 1947). The pelecypod material includes two species of a mytiloid; Eumicrotis, Gryphea cf. G. nebrascensis, and Ostrea strigilecula of the Ostreacea. The brachiopod Lingula brevirostris has also been described from the Stockade Beaver Shale. These organisms are generally considered to be indicators of a shallow marine to brackish water environment with fairly low levels of silting, because these animals were essentially sedentary with an easily clogged filtering aparatus. Bobb Schaeffer has been collecting well preserved fish from these deposits as well (per. comm.).

Imlay (1947) indicates that the Lower Callovian in North America was marked by a transgression from the east, established by sediment correlations to the east and southeast, at which time the Stockade Beaver Member was deposited. The sediments consist primarily of a normal marine gray shale. Barnard (1973) cites evidence indicating that the area under consideration lay near the equator during the Upper Jurassic, i.e. evaporite belts in this region along with terrestrial tetrapod faunas taken to be warm-adapted imply that the climate was tropical or subtropical at that time. The organisms found in the Stockade Beaver Member of the Sundance Formation, then, lived in a warm, shallow marine or brackish environment that seems to have been unstable with respect to sedimentation, because Mecochirus and the glypheid appear to have been quickly buried alive. Antrimpos

and Bombur were dead and slightly decomposed at the time of burial, perhaps due to the rapid development of anoxic conditions.

Because most of the known Jurassic fossil decapod material has been described from Europe, it is worthwhile to consider what occurred there during the Callovian and Oxfordian. Central Germany apparently was a deep basin; the sediments consist of marls, indicative of a deep-water environment (Gignous, 1955). This basin was directly connected with the Anglo-Parisian Basin, and there were connections with the Russian Basin as well. During the Callovian-Oxfordian, cold waters from the North Sea region apparently drained into the German and Anglo-Parisian Basins so that these areas were included in the northern boreal province first described by van Straelen (1925) and later by Gignoux (1955).

The classic European collecting sites in the Callovian and Oxfordian (Germany, England, and France), provided an unfavorable environment for the knids of organisms preserved in the Stockade Beaver Shale, since the latter animals appear to have been adapted to tropical or subtropical, shallow marine environment, whereas the major part of Jurassic Europe was the site of a deeper coldwater basin. Some palinurids have been reported from Europe, however; Pseudoglyphea eximia and P. terquemi being reported from the Oxfordian of east France; and Mecochirus socialis, Callovian-Oxfordian in age from south and north Germany, north and southeast France, and south England; along with Mecochirus pearci from the Oxfordian in south England, have also been descrobed (Förster, 1971).

Decapod faunas similar to the Stockade Beaver material have been reported from other times when conditions were more favorable for such organisms. Pinna (1967) described an assemblage dating from the Lias of Italy (Lower Jurassic) that consisted of the penaeid Aeger; two palinurids, Coleia and Knebalia; and an astacid, Eryma. Another Italian deposit of Norian age (Upper Triassic), contains two penaeids, Antrimpos and Aeger; and unidentified caridean and an astacid; the palinurid Protoclytiopsis is also included (Pinna, 1973). This latter assemblage was described from the Zorzino Limestone, a gray, shallow marine deposit somewhat similar to the Stockade Beaver Member. Although the sediments are coarser, the environments of both regions seem to have been tropical or subtropical, shallow marine areas.

An Upper Triassic (Karnian) assemblage of decapods was described from the Raibler Series of Germany, including the penaeids Antrimpos straeleni and Bombur(?) aonis; and astacid Clytiella spinifera, and the palinurids Pseudoglyphea mulleri and Glyphea(?) tantalus (Förster, 1967), from a region which in Karnian time was warm and produced lagoonal sediments (Gignoux, 1955). The environment and fauna were not too different from those of the Stockade Beaver Shale.

The German lithographic limestones from the Solenhofen quarries, Lower Portlandian in age (Jurassic-Cretaceous boundary) show unusually fine preservation of a number of phyla not ordinarily preserved as fossils. A large assortment of crustaceans were described from the Solenhofen, including hoplocarids, peracarids, mysids, and isopods. A large number of eucarids were also preserved, including several

species of Antrimpos, Bombur, two glypheids (Glyphea squamosa and G. pseudosyllaris), several mecochirids, and many other forms. Most of the major malacostracan groups were represented in these sediments, but such is rarely the case, because soft-bodied forms like those found in the Solenhofen limestones were usually disarticulated and decomposed before they could be preserved. The environment of deposition of the Solenhofen sediments was warm, shallow marine, and lagoonal, perhaps marked by atolls (Gignoux, 1955).

The Francis Creek Shale, Pennsylvanian in age, can be compared to the Solenhofen because preservation of soft-bodied forms was unusually good. Although no decapodous crustaceans have been described from this deposit, an extensive fauna of the more primitive malacostracans are known, including phyllocarids and hoplocarids, as well as peracarid, syncarid, and eocarid eumalacostracans. The North American Bear Gulch fauna, dating from Mississippian, is similar to the Francis Creek assemblage as far as type of preservation is concerned. Again, the environment of deposition for both of the above are comparable to that of the Stockade Beaver Shale, although conditions were not quite as good for the preservation of soft-bodied forms, and the crustacean elements are quite different from those of Mesozoic age.

A general trend might be noted in the decapodous crustaceans. The earliest record dates from the Devonian; after extensive radiations through the Triassic, the group stabilized and became static until the Triassic and then again in the Cretaceous, at which time much diversifi-

cation took place. The earliest true decapod, Palaeopalaemon, with closest affinities to the glypheoid palinurans, dates from the Late Devonian (Schram, et al, in press). Another Paleozoic decapod, an astacid, Protoclytiopsis antiqua was described from the Upper Permian (Birshteyn, 1958). Most of the major primitive decapod groups, the penaeids, palinarids, and astacids, became firmly established during the Triassic and were the dominant forms during the Jurassic (Pinna, 1967, 1969, 1973a, b, and c; Schram, 1971), and were then replaced by more advanced forms such as the anomurans and brachyurans (Bishop, 1972; Förster, 1968, 1970b) during the Cretaceous, at which time extensive radiations began in the latter groups as many of the former groups began to decline.

It seems that the decapods found in the Stockade Beaver Member of the Sundance Formation, Wyoming, are a typical early Mesozoic group of crustaceans living in a shallow, tropical or subtropical, marine environment. The area does not appear to have been particularly stable in that some of these shrimps were quickly buried alive, and others seem to have been killed in large numbers and were partially decomposed before they were buried. The Stockade Beaver fauna is comparable to faunas described from European deposits Triassic and Jurassic in age, and is the only Jurassic crustacean fauna known in North America to date.

Table 1

Some representative individual measurements, in mm, of the Stockade Beaver material. In most cases, figures are best approximations of true values because the specimens were not preserved intact.

	Pl	Cp	Ab	l	b	Ant f
36245 (*Antrimpos* sp.)		16.9	34.2			
36261 (*Bombur* sp.)		7.6	16.7			
36264a (*Mecochirus* sp.)	11.0	7.4(?)	8.9			
36265 (*Mecochirus* sp.)	21.2(?)	14.7(?)	13.3			
36267 (Anomuran)				12.5	8.0	
36268 (Anomuran)				11.2	6.5	
36270 (Glypheoid)	22.0					17.5

Abbreviations: Pl, first pereiopod measured from dactylus to carapace margin; Cp, carapace measured from base of rostrum to posterior of abdomen; Ab, abdomen exclusive of telson; Ant f, antennular flagellum; l, length across carapace (maximum); b, breadth of carapace (maximum).

Explanation of Figures

FIG. 1. a. *Antrimpos* sp., composite reconstruction from all material at hand.

b. Unidentifiable anomuran material, specimen 36267.

c. Unidentifiable anomuran material, specimen 36268; assumed to be part of a thoracopod manus.

d. *Bombur* sp., composite reconstruction from all material at hand.

e. *Mecochirus* sp., composite drawing of material at hand.

f. Glypheoid decapod, genus uncertain, specimen 36270; P_1 is first pereiopod; a branchiocardiac groove; c, postcervical groove.

Scale represents 1 cm.

FIG. 2. a. *Mecochirus* sp., specimen 36265, X2.5.

b. Unidentifiable anomuran material, specimen 36267, X3.3.

c. *Mecochirus* sp., specimen 3624A, X2.8.

d. *Antrimpos* sp., specimen 36245a, X1.8.

Scale represents 1 cm.

FIG. 3. a. *Bombur* sp., specimen 36261a; tu, telson plus uropods; X2.9.

b. *Bombur* sp., specimen 36263, X2.8.

c. Unidentifiable anomuran material, specimen 36268, X3.1.

d. Glypheoid decapod, genus uncertain, specimen 362670; P_1, first pereiopod; a, branchiocardiac; c, postcervical; X2.4.

Scale represents 1 cm.

FIG. 4. Unidentifiable glypheoid, specimen 36271A, assumed to be generic with specimen 36270; X3.6.

Scale represents 1 cm.

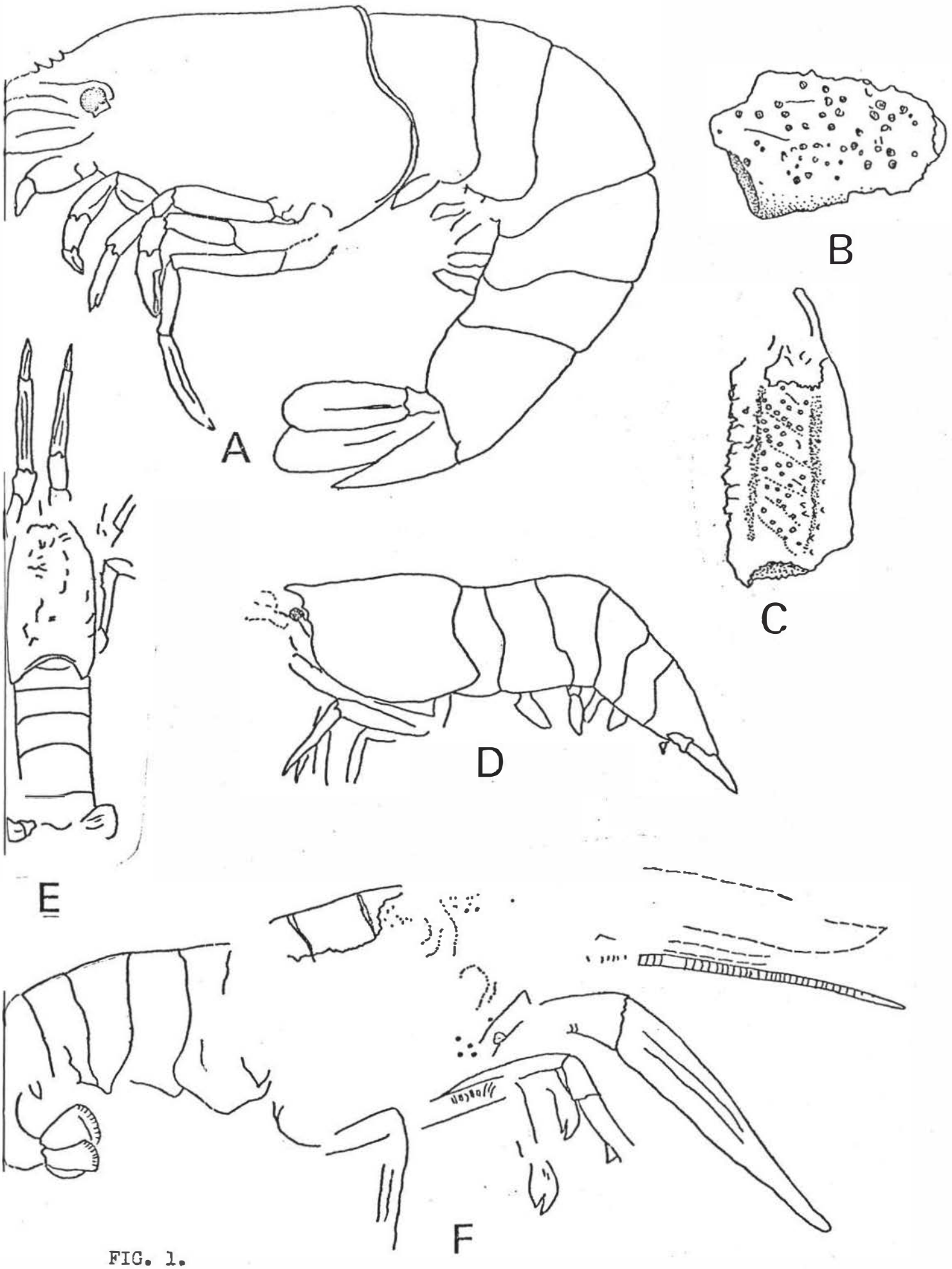
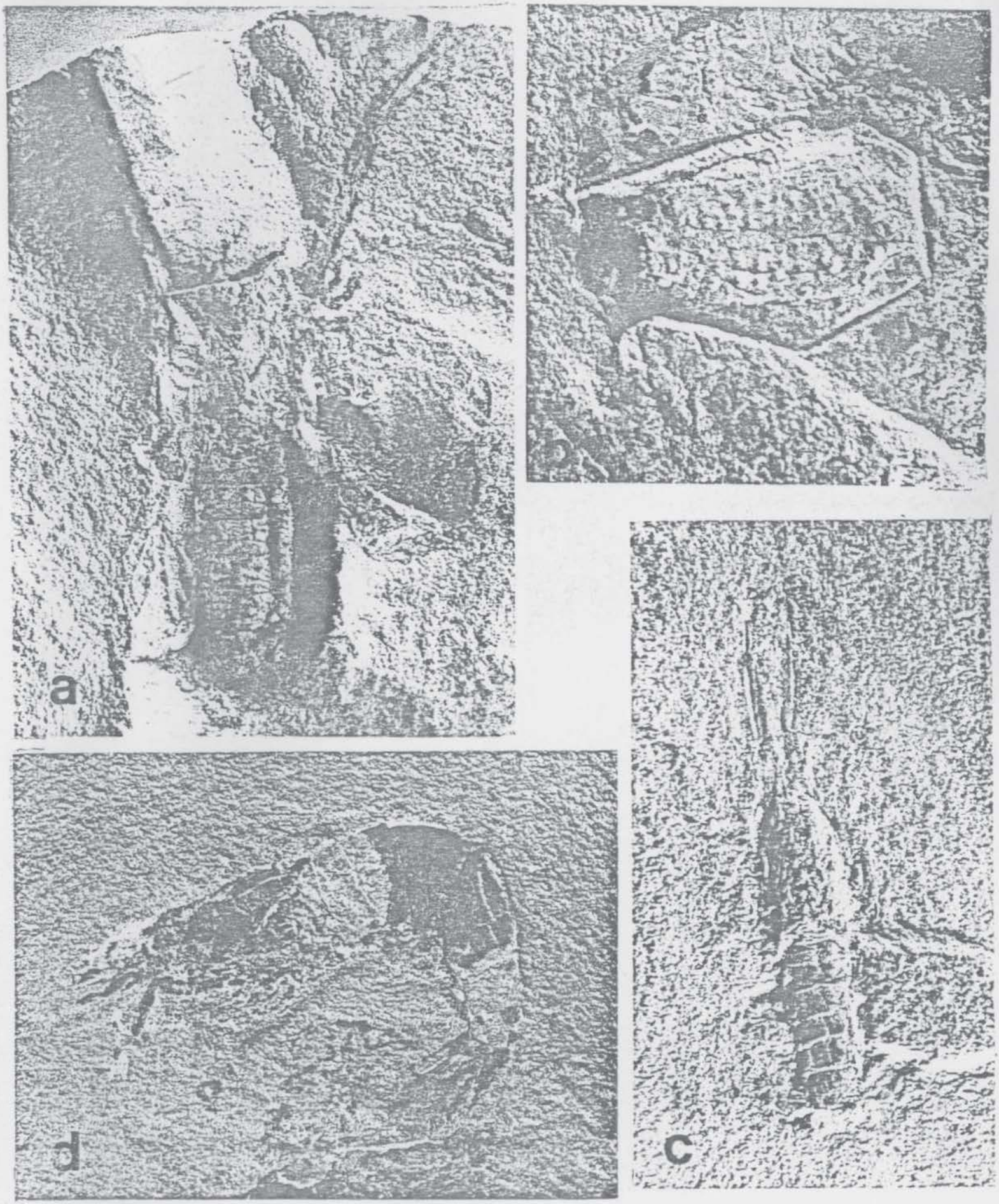


FIG. 1.


a
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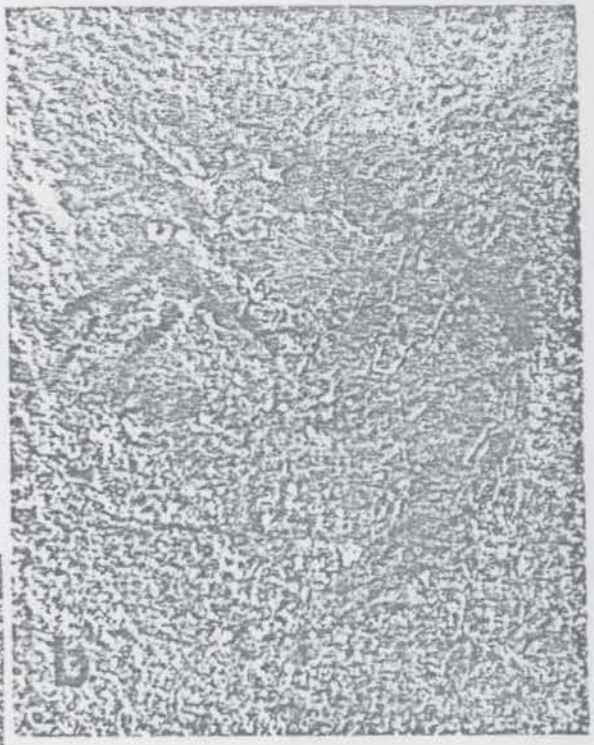
d



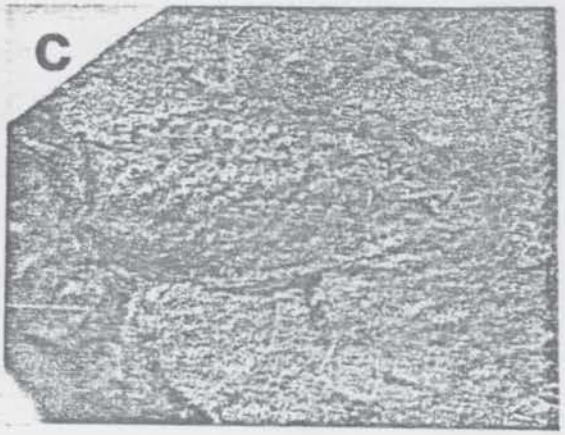
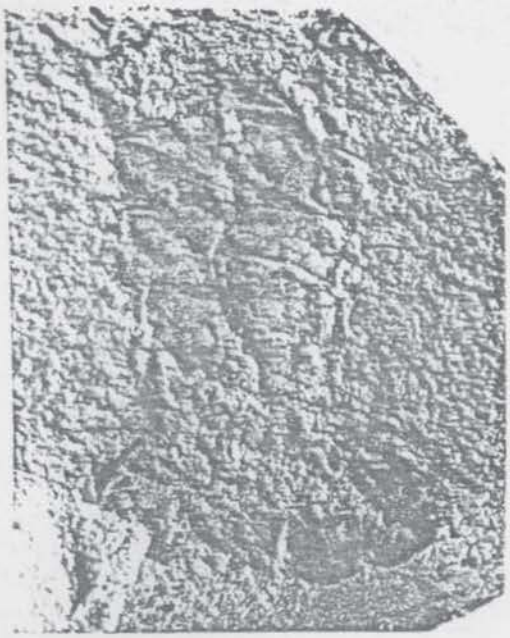


Fig. 4



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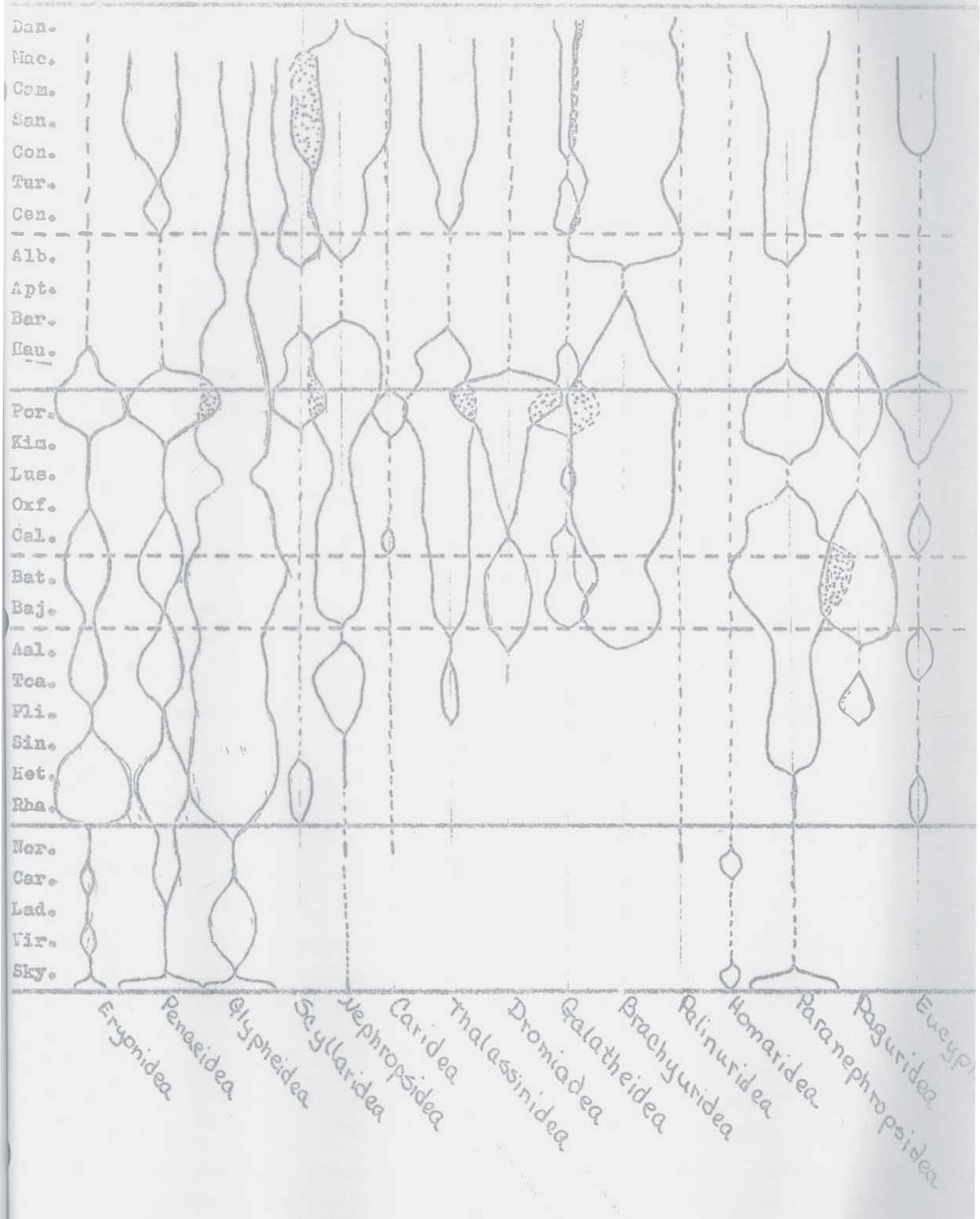
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Dromiadea
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Brachyuridea
Palinuridea
Homaridea
Paranephropsidea
Paguridea
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Upper Cretaceous	Danian			
	Senonian	Aturian	Maestrichtian	
			Campanian	
		Emscherian	Santonian	
			Coniacian	
	Turonian			
	Cenomanian			
Lower Cretaceous	Albian = Gault			
	Aptian			
	Barremian			Neokom
	Hauterivian			Neokom
Upper Jurassic	Portlandian = Tithonian			Malm
	Kimmeridgian			Malm
	Lusitanian			Malm
	Oxfordian			Malm
	Callovian			Malm
Middle Jurassic	Bathonian			Dogger
	Bajocian			Dogger
Lower Jurassic or Lias	Aalenian			
	Toarcian			
	Pliensbachian = Charmouthian			
	Sinemurian			
	Hettangian			
	Rhaetian			

Triassic	Alpine Type	Germanic Type
	Norian	Keuper
	Carnian	Keuper
	Ladinian	Muschelkalk
	Virglorian or Anisian	Muschelkalk (≈ Wellenkalk)
	Werfenian or Skythian	Buntsandstein

From Gignoux, M., Stratigraphic Geology; W.H. Freeman and Co., San Francisco and London; 1955, p. 265-466. Transl. G.G. Woodford.