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Malacostracan Crustacean Fauna from the Sundance Formation (Jurassic) of Wyoming

ELIZABETH M. HERRICK¹ AND FREDERICK R. SCHRAM²

ABSTRACT

The only marine Jurassic decapod fauna in North America is found in the Stockade Beaver Member of the Sundance Formation of Wyoming. The preservation of these crustaceans is only moderately good, permitting, at most, identification to the generic level of these soft-shelled decapod shrimp. The faunal

assemblage, composed of *Antrimpos* sp., *Bombur* sp., *Mecochirus* sp., a glypheid, and some unidentifiable anomuran remains, can be compared with Triassic and Jurassic material from European deposits, which form part of the biologic continuum of crustaceans throughout the Lower Mesozoic.

INTRODUCTION

Strata of marine Jurassic age are not abundant for the most part in the United States, one of their principal outcrops being in the Black Hills area, South Dakota, and somewhat westward in Wyoming. Much of North America was subaerially exposed during the Jurassic and no sediments of marine origin were deposited (Gignoux, 1955; Hallam, 1969; Imlay, 1965). 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 by Bobb Schaeffer from the Stockade Beaver Member of the Sundance Formation from Bush Canyon, 2.5 miles north of Hulett in Secs. 25 and 36, T55N, R65W, Crook County, Wyo-

ming; and are deposited in the American Museum of Natural History.

The Sundance Formation consists of five members, and has a range of 75 to 115 m. (200 to 350 ft.) 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 15 m. (50 ft.) in thickness, although it ranges from 1.5 to 26 m. (5 to 85 ft.) (Imlay, 1947; Wright, 1973). The Stockade Beaver 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 siltstone and

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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 lagoonal, 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 decomposed before they could be buried. A number of soft-shelled, intact decapod shrimp have been found. The Stockade Beaver Shale is the only known source of Jurassic decapod material in North America.

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 exterior 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 number of individuals.

ACKNOWLEDGMENTS

We thank Dr. Bobb Schaeffer of the American Museum of Natural History for bringing the material to our attention and for allowing us to describe it. The manuscript was read and criticized by Drs. R. M. Feldmann, Kent State University, Ohio, and J. F. Stratton, Eastern Illinois University. The work was supported by grants from the Eastern Illinois University Council on Faculty Research.

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.

Figures 1A; 2D

Description of Specimens. AMNH 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 (AMNH 36245a, 36257a, 36259a, fig. 2D). The body is laterally compressed and the carapace is thin and uncalcified with a marginal ridge (AMNH 36247a). No grooves or other surface ornamentation were preserved. The pereopods are long and slender; the merus seems to be slightly longer than each of the remaining segments, but the poor preservation prevents actual measurement or absolute size comparisons. The first three pereopods are chelate, and pereopods 4 and 5 exceed the first three in length (AMNH 36259a). There are no spines or any other ornamentation of the pereopods. The scaphocerite is large and oval. No other details of the antennae are discernible.

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 (AMNH 36259). The telson is triangular and the uropods are leaf-shaped without a diarsis (figs. 1A, 2D). Only the proximal portion of the pleopods is preserved.

Remarks. Out of some 45 individuals, no one specimen was preserved totally. The above description and reconstruction (fig. 1A) is based on a composite. None of the specimens has a complete rostrum, although it is partially preserved on AMNH 36245a, 36257a, and 36259a. The posterior portion of the carapace showing the doublure in most cases has been obliterated. These animals were buried as

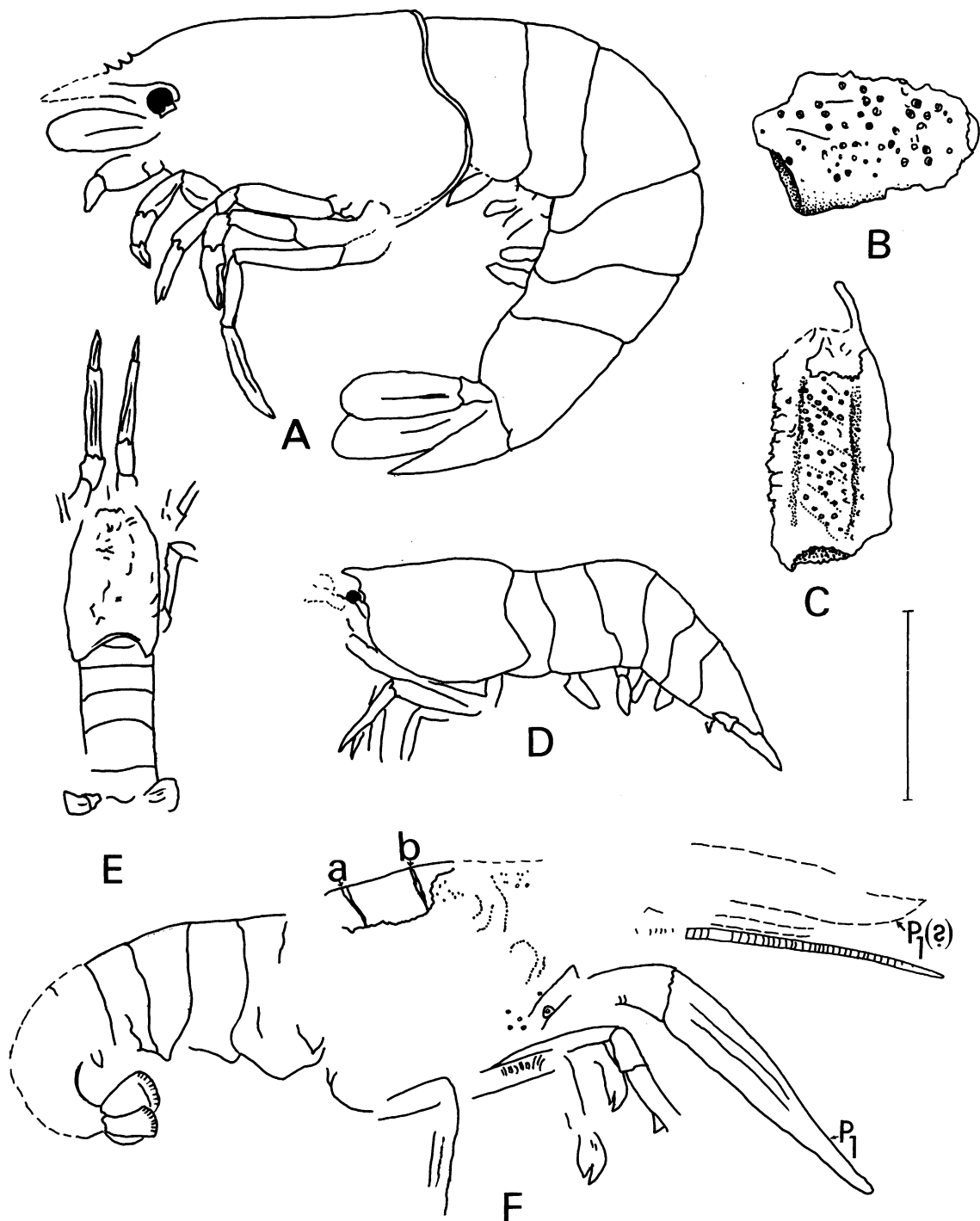


FIG. 1. A. *Antrimpos* sp., composite reconstruction based on all material available. B. Unidentifiable "anomuran," AMNH 36267a. C. Unidentifiable "anomuran," AMNH 36268a, assumed to be part of a thoracopod manus. D. *Bombur* sp., composite reconstruction based on all available material. E. *Mecochirus* sp. composite reconstruction based on all material available. F. Glypheoid decapod, genus uncertain, AMNH 36270; p_1 = first pereiopod, a = branchiocardiac groove, b = postcervical groove.

Scale represents 1 cm.

whole organisms rather than as exuviae, since the carapace does not show any evidence of molt suture. Nor is any specimen in the Salter position (Bishop, 1972), i.e., with carapace up at an angle of 45 degrees with respect to the abdomen. The coxal and basal segments of the pereopods are not visible, and the pereopods 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 pereopods 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 pereopods 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.

Figures 1D; 3A, B

Description of Specimens. AMNH 36257b, 36258, 36261a, and 36263. These specimens were small forms with a simple, short, blunt rostrum (AMNH 36261a, fig. 3A). The body is laterally compressed. The carapace is thin, uncalcified, and smooth. Pereopods 4 and 5 are long, slender, and achelate. There are not discernible details for any of the other pereopods (AMNH 36263, fig. 1D). Antennular details are lacking on all specimens. The eye stalk can be seen on AMNH 36261a, along with a perorbital 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 (AMNH 36257b).

The telson appears to be triangular (AMNH 36261a, fig. 3B).

Remarks. The cuticle of these animals was apparently very thin and did not preserve well. Two specimens (AMNH 36263 and 36257b) have lost large portions of the integument and are preserved only as molds. The pereopods in most cases have not been preserved at all, although two appendages can be seen on 36263. They are taken to be pereopods 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 sclerotized and are folded against the telson, and thus were poorly preserved (AMNH 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 larger 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 is poorly known. Glaessner (1969) stated 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 details such as the rostrum and the preorbital spine, along with some indication of the structure of some of the appendages, for example pereopods 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.

Figures 1E; 2A, 2C

Description of Specimens. AMNH 36264a,

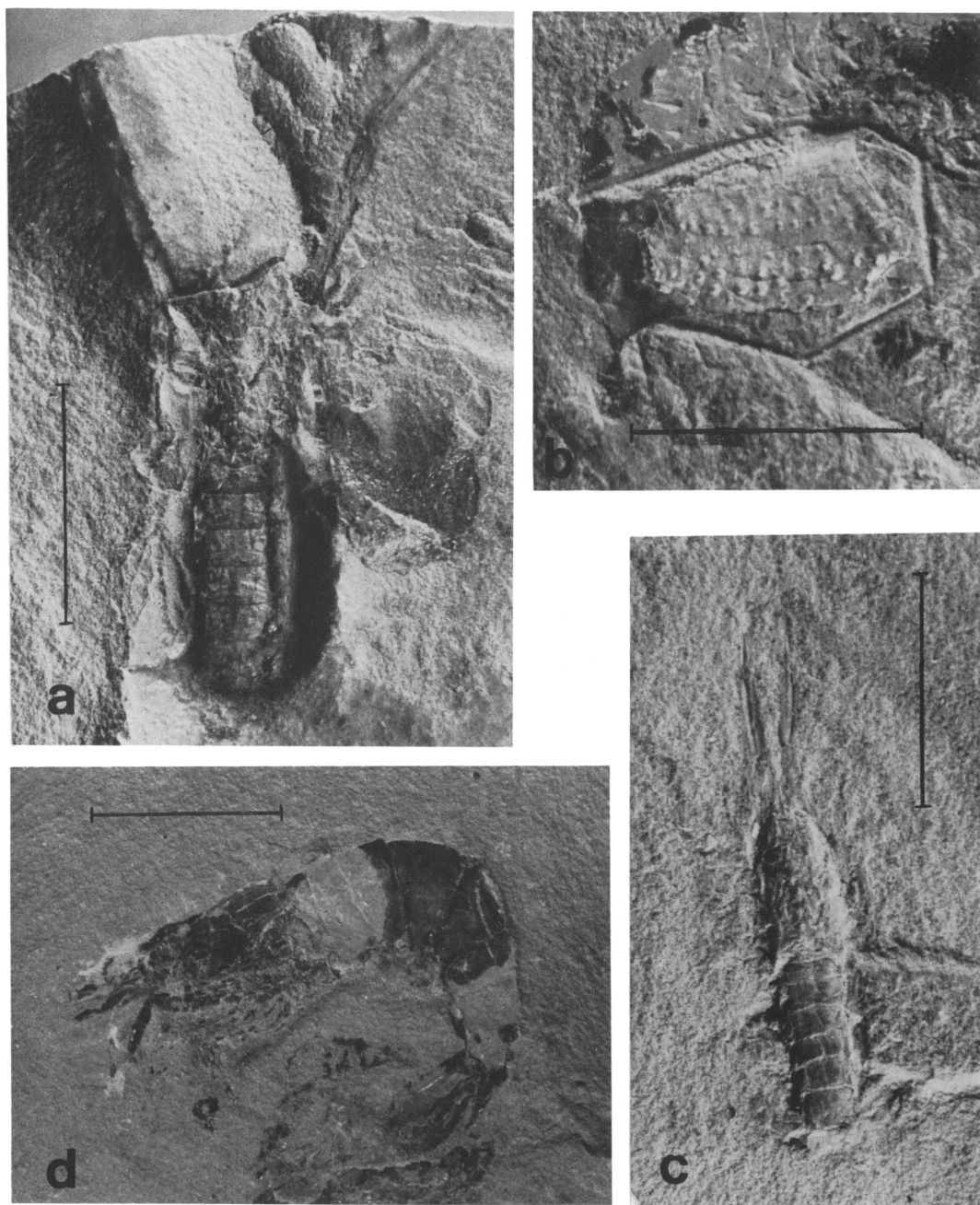


FIG. 2. A. *Mecochirus* sp., AMNH 36265. B. Unidentifiable "anomuran," AMNH 36267a. C. *Mecochirus* sp., AMNH 36264a. D. *Antrimpos* sp., AMNH 36245a. Scales represent 1 cm.

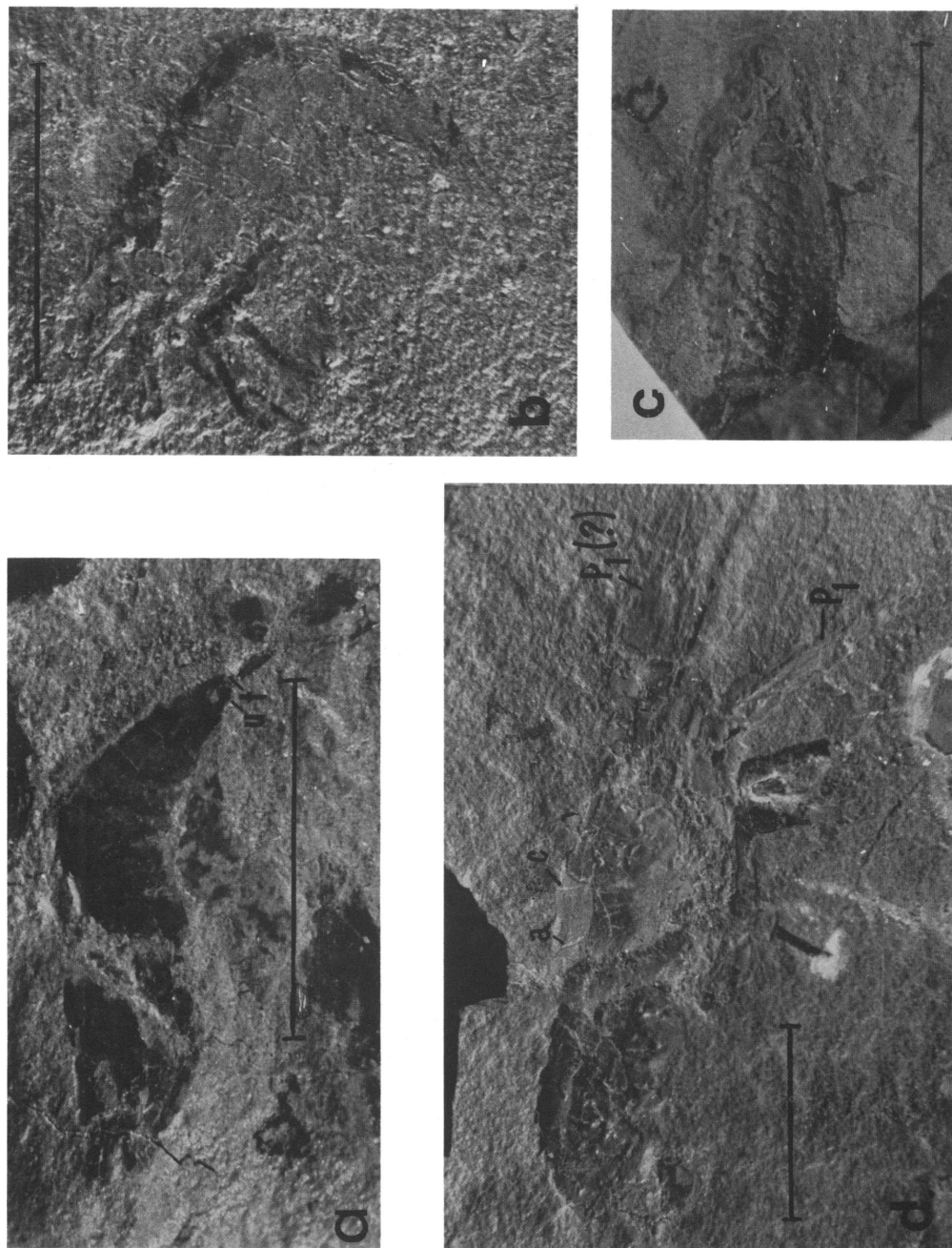


FIG. 3. A. *Bombur* sp., AMNH 36261a; tu = telson and uropods. B. *Bombur* sp., AMNH 36263. C. Unidentifiable "anomuran," AMNH 36268a. D. Glyphceoid decapod, genus uncertain, AMNH 36270; P_1 = first pereiopod, a = branchiocardiac groove, c = postcervical groove.
Scales represent 1 cm.

36264b, and 36265. The carapace is subcylindrical and very thin. Only the branchiocardiac and postcervical grooves were preserved and are partially visible. The first pereopods are long and slender, and apparently subchelate (fig. 2A and C). The first pereopods of 36264a are approximately half the length of the body, measuring an estimated 11 mm. as compared with 17 mm. for the body, measured from the approximate base of the rostrum to the telson. The first pereopods of AMNH 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 coxa and basis were not preserved. The anterior portion 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 AMNH 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 and apparently with a diaresis.

Remarks. The material available consists of two incomplete individuals (AMNH 36264a and 36264b, and 36265), and possibly a third very poorly preserved specimen (AMNH 36266a and 36266b). The anterior portion of the carapace was badly preserved and distorted and thus does not allow a determination of the characteristic propodus-carapace length ratio, so these organisms cannot be assigned to a specific species. The subchelate nature of the first pereopods is clearly illustrated on AMNH 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 (figs. 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 pereopods, and the smooth, thin carapace, along with the apparent position of the branchiocardiac and postcervical grooves. The above characteristics serve to distinguish *Mecochirus*

from its more heavily calcified relative *Meyeria* [Förster (1971) believes *Meyeria* may be synonymous with *Mecochirus* but Feldmann (personal commun.) disagrees] and *Pseudoglyphea* with its shorter, more robust, and spinous first pereopod.

FAMILY GLYPHEIDAE WINKLER, 1883

GENUS UNCERTAIN

Figures 1F; 3D

Description of Specimens. AMNH 36270, 36271a, and 36271b. The carapace was well sclerotized and the body subcylindrical. Only portions of the branchiocardiac and postcervical grooves were preserved. The first pereopods 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 pereopod appears to be subchelate, and the third is chelate (AMNH 36270, fig. 1F). The antennular flagellum is moderately long, approximately as long as the first pereopod. Tubercles might be present on the anterior portion of the carapace, but preservation is poor and most of the details were obscured. No other ornamentation of the carapace or pereopods was preserved.

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

Remarks. The description is largely based on specimen AMNH 36270; however, AMNH 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 pereopods, making it difficult to assign this animal to the generic level.

None of the appendages were preserved on AMNH 36271. Although the first pereopod of AMNH 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 pereopods. The chelate nature of the third pereopod can clearly be seen (fig. 1F), but the distal portion of the second pereopod was not well preserved and it is difficult to determine whether the appendage is subchelate or chelate; however, it is clearly not achelate (fig. 3D). These animals appear to be glypheoids, based on the flattened first pereopods, the position (?) of branchiocardiac and postcervical grooves, and the structure of the abdomen.

UNIDENTIFIABLE MATERIAL

Description of Specimens. AMNH 36267a and 36268a. Also included in the Stockade Beaver crustaceans are two fragments of heavily calcified decapod remains (AMNH 36267a and 36268a). One fragment (AMNH 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. (Dr. R. M. Feldmann has a specimen from these deposits of an erymid of which this carapace fragment may be an example.)

The second fragment (AMNH 36268a, fig. 3C), seems to be a part of a thoracopod manus. There is a raised central portion with diagonal

TABLE 1
Some Representative Individual Measurements (in Millimeters)
of the Stockade Beaver Material

	Pl	Cp	Ab	l	b	Ant.f
36245	—	16.9	34.2	—	—	—
(<i>Antrimpos</i> sp.)						
36247a	—	—	29.0	—	—	—
(<i>Antrimpos</i> sp.)						
36249	—	14.0	31.9	—	—	—
(<i>Antrimpos</i> sp.)						
36254	—	13.3	—	—	—	—
(<i>Antrimpos</i> sp.)						
36257b	—	6.5	12.5	—	—	—
(<i>Bombur</i> sp.)						
36261	—	7.6	16.7	—	—	—
(<i>Bombur</i> sp.)						
36263	—	6.0	12.1	—	—	—
(<i>Bombur</i> sp.)						
36264a	11.0	7.4(?)	8.9	—	—	—
(<i>Mecochirus</i> sp.)						
36265	21.2(?)	14.7(?)	13.3	—	—	—
(<i>Mecochirus</i> sp.)						
36267a	—	—	—	12.5	8.0	—
(erymid ?)						
36268a	—	—	—	11.2	6.5	—
(anomuran ?)						
36270	11.0	—	—	—	—	17.5
(glypheoid)						

In most cases, figures are best approximations of true values because the specimens were not preserved intact.

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



FIG. 4. Unidentifiable glypheoid, AMNH 36271a, assumed to be congeneric with AMNH 36270.

Scale represents 1 cm.

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 AMNH 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 bivalves, 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 is dominated by *Meleagrinea curta* but includes two species of a mytiloid, *Eumicrotis*, *Gyphea* cf. *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 rates of silt accumulation because these animals were essentially sedentary with an easily clogged filtering apparatus. Abundant palaeoniscoid fish remains have also been recovered from these deposits (Schaeffer, personal commun.). Wright (1973) indicated an open shallow shelf environment in the Crook County area in Callovian-Oxfordian time.

Imlay (1947) indicated 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) cited 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 characterized by episodes of rapid sedimentation, because *Mecochirus* and the glypheid appear to have been quickly buried alive.

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 (Gignoux, 1955). This basin was directly connected with the Anglo-Parisian Basin, and there were connections with the Russian Basin as well. During Callovian-Oxfordian time, 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). Imlay (1965) suggested Arctic cooling as a mechanism for Jurassic faunal differentiation, although Hallam (1969)

claimed that decreases in salinity were more important.

The classic European collecting sites in the Callovian and Oxfordian (Germany, England, and France) represented environments rather different from those that apparently existed during deposition of the Stockade Beaver Shale. The animals from the latter deposit appear to have been adapted to a tropical or subtropical, shallow marine environment, whereas the major part of Jurassic Europe was the site of a somewhat deeper, cold-water basin (Hallam, 1969). The European crustacean fauna is particularly rich in palinurids: *Pseudoglyphea eximia* and *P. terquemi* being reported from the Oxfordian of east France; *Mecochirus socialis*, Callovian-Oxfordian in age, from south and north Germany, north and southeast France, and south England; and *Mecochirus pearci* from the Oxfordian in south England (Förster, 1971).

Decapod faunas similar to the Stockade Beaver material have been reported, however, 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 specimens of the penaeid *Aeger*; two palinurids, *Coleia* and *Knebalia*; and an astacid, *Eryma*. Another Italian deposit of Norian age (Upper Triassic) contains specimens of two penaeids, *Antrimpos* and *Aeger*, an unidentified caridean and an astacid; the palinurid *Proctoclytiopsis* 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*; the astacid *Clytiella spinifera*, and the palinurids *Pseudoglyphea mulleri* and *Glyphea* (?) *tantalus* (Förster, 1967), from a region which, in Karnian time, was apparently warm and accumulated lagoonal sediments (Gignoux, 1955). The environment and fauna were not too dif-

ferent 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 (e.g., Münster, 1839; or Oppel, 1862), including hoplocarids, peracarids, mysids, and isopods. A large number of eucarids are 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 not usually the case, because soft-bodied forms like those found in the Solenhofen Limestone were usually disarticulated and decomposed before they could be preserved. In general, the Mesozoic crustacean faunas are dominated by diverse decapod eucarids and exhibit wide ecological and biogeographic distribution.

The Mesozoic faunas are quite different and distinct from the Late Paleozoic faunas (Schram, 1977). The Late Paleozoic faunas have an extensive array of the more primitive malacostracans such as phyllocarids and hoplocarids, as well as primitive peracarid, syncarid, and eocarid eumalacostracans. These Late Paleozoic faunas, largely confined to Laurentia, stand in strong contrast to the more ubiquitous, largely decapod and advanced peracarid faunas of the Mesozoic.

A general trend might be noted in the evolution of decapod crustaceans. The earliest record dates from the Devonian, and after an initial radiation through the Triassic the group stabilized and became static until the Cretaceous, at which time much diversification took place. The earliest true decapod, *Palaeopalaemon*, with close affinities to both the glypheoid palinurans and astacideans, dates from the Late Devonian (Schram, Feldmann and Copeland, in press); and another Paleozoic decapod, an astacid, *Proctoclytiopsis antiqua*, was described from the Upper Permian (Birshteyn, 1958). Most of the major primitive decapod groups, the penaeids, palinurids, and astacids, became

firmly established during the Triassic and were the dominate forms during the Jurassic (Pinna, 1967, 1973; Förster, 1973a, 1973b, and 1973c; Schram, 1971). These were then replaced by more advanced forms in the Cretaceous, such as the anomurans and brachyurans (Bishop, 1972; Förster, 1968, 1970b), with many of the Early Mesozoic groups in 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 that lived in a shallow tropical or subtropical marine environment. The Stockade Beaver fauna, the only Jurassic crustacean fauna known in North America to date, is comparable with shallow-water European Triassic and Jurassic deposits, that possess genera like *Antrimpos*, *Bombur*, *Mecochirus*, and groups like glypheoids and erymids. Schram (in press) has discussed the faunal development of Late Paleozoic malacostracans and shown how consistent assemblages of shrimp had persisted and evolved as chronofaunas through that time. The comparison of the Stockade Beaver crustaceans with other crustacean assemblages of the Triassic and Jurassic seems to indicate that chronofaunas of these shrimp may also have been in existence during the early Mesozoic.

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