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Ophiomorpha and a New Thalassinid Burrow from the Permian of Utah

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ABSTRACT.—Two excellent examples of thalassinid decapod burrows were recently discovered in the Permian Cedar Mesa Sandstone of the Colorado Plateau. One of these burrows is the earliest known occurrence of *Ophiomorpha nodosa* Lundgren. *Ophiomorpha nodosa* is a well-known burrow made by the extant thalassinid decapod *Callianassa major* Say. *Callianassa* is not known to have occurred before the Upper Jurassic and the previous known occurrence of *Ophiomorpha* was Middle Jurassic through Holocene.

The new burrow *Ardelia socialia* was probably made by an early thalassinid as well. *Ardelia* is profuse in a local area and is associated with the *Ophiomorpha* burrows. *Ardelia* consists of numerous small tubes 3 to 7 mm in diameter that branch radially from a central gallery and extend 5 to 10 cm outward to build up a large, composite, nodular structure 10 to 20 cm in diameter. They are vertical, horizontal, and oblique and have been traced for more than two meters.

Boxwork burrows are most common in bays, lagoons, and tidal flats. *Ardelia* and *Ophiomorpha* of this report are boxwork-deposit feeding patterns. Therefore, it is concluded that the Cedar Mesa Sandstone bearing these burrows was deposited in a tidal-flat environment.

Because the evidence from body fossils indicates that the decapods did not evolve until Late Permian or Early Triassic, several important questions remain unanswered as to the relationship of these Permian burrows to known fossorial shrimp and to the Jurassic and younger thalassinid burrows.

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INTRODUCTION

The extant ghost shrimp *Callianassa major* Say (Callianassidae, Thalassinoidea, Decapoda) makes a distinctive trace fossil called *Ophiomorpha nodosa*

Lundgren consisting of a tube with a nodose, pelleted wall. *O. nodosa* has proven to be a useful trace fossil because it is distinctive and because it is restricted mainly to the beach environment (Weimer and Hoyt, 1964; Hoyt and Weimer, 1965).

The main purpose of this paper is to describe a new and very early occurrence of *Ophiomorpha nodosa* and another probable thalassinid burrow, *Ardelia socialia* n. ichngn.-sp. in the Permian Cedar Mesa Sandstone of Utah. *O. nodosa* discovered by us in the Wolfcampian Cedar Mesa Sandstone of the Colorado Plateau of Utah is particularly interesting because (1) the oldest known decapods are Permotriassic (Glaessner, 1969; Brooks, 1969; Burkenroad, 1963), (2) the known range of *Callianassa* is Upper Jurassic (Rathburn, 1926) or Lower Cretaceous through Holocene (Glaessner, 1969), and (3) the previous known range of *Ophiomorpha nodosa* was Middle Jurassic through Holocene (Heinberg, 1970; Häntzschel, 1962).

The occurrence of (1) *Ophiomorpha* from the lower Upper Permian Zechstein (A. Seilacher, 1972, oral communication to Chamberlain) and from the Wolfcampian White Rim Sandstone of the San Rafael Swell of Utah and of (2) the *Ophiomorpha*-like *Walpia* White (Häntzschel, 1962) from the Leonardian Hermit Shale of Arizona provides additional reason to believe that the Cedar Mesa form is also *Ophiomorpha* and not just diagenetic structures (Häntzschel, 1971, written communication to Chamberlain).

Glaessner (1969) believed the Thalassinoidea to be a branch of the Glypheoidea, but Burkenroad (1963) believed that the Thalassinoidea originated from a Triassic thalassinid-like decapod and that Glypheoidea were an early offshoot. Based on the present stratigraphic evidence of body fossils, the Glypheoidea are known from older rocks (Lower Triassic [?] or Middle Triassic) than the Thalassinoidea (Lower Jurassic) and have been found in the burrow *Thalassinoides* in older rocks than have the Thalassinoidea. Brooks (1969), Burkenroad (1963), and Glaessner (1969) discuss the morphologic and biologic factors bearing on decapod phylogeny, and the reader is referred to them for these details. A significant bias may have been introduced into present interpretations by lack of preservation or discovery of important forms. Preservation is not common in decapods, particularly in the geologically older cryptic shrimp, because these forms did not strongly calcify their carapace. More commonly it was the geologically younger forms that developed this specialization, and strongly calcified chelae are frequently found. It is not surprising that many burrows have an older known geologic range than the animals responsible for the burrow.

The second purpose of this paper is to pose and speculate on the following problems:

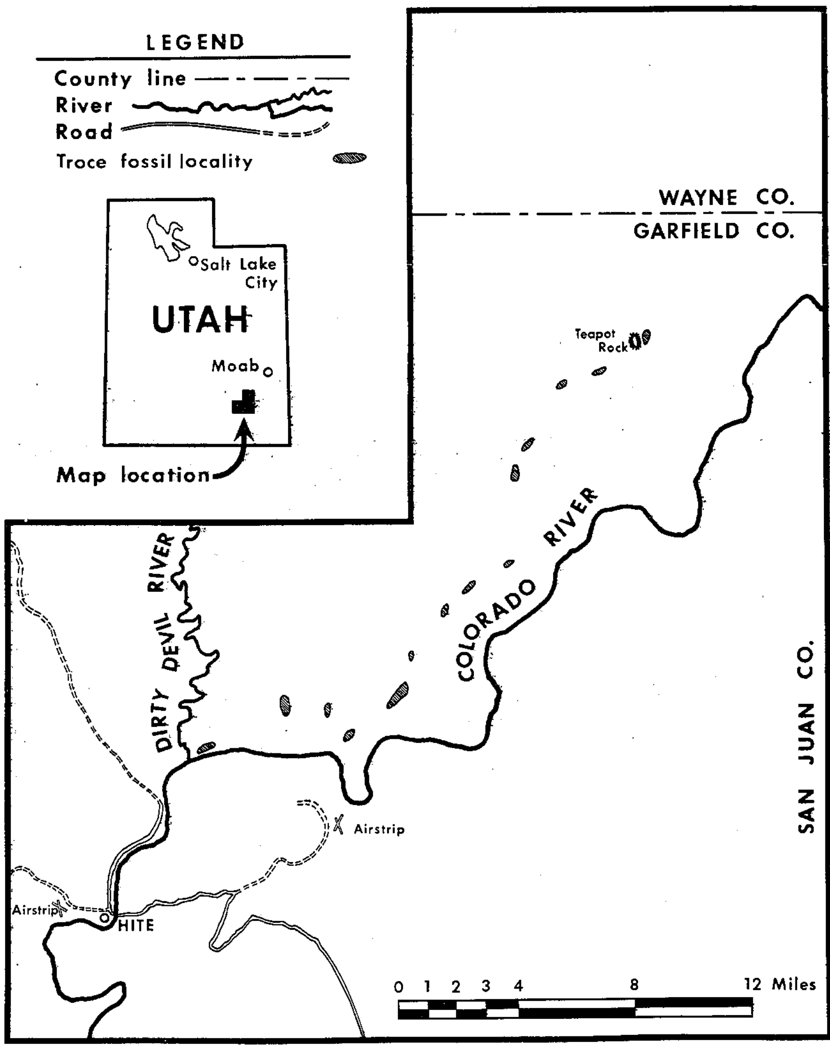
1. Were these Permian burrows made by decapods?
2. Were the Permian *Ophiomorpha* made by a direct-line species of *Callianassa*?
3. Do these burrows provide evidence for the development of the Thalassinoidea beginning in the Permian or Pennsylvanian—earlier than was previously thought?

ACKNOWLEDGMENTS

Thanks are given to John W. Warme, of Rice University, for reading the manuscript and making useful suggestions, and to Dean Davidson, of Utah State University, for providing some of the specimens used in this study.

TRACE-FOSSIL LOCALITIES

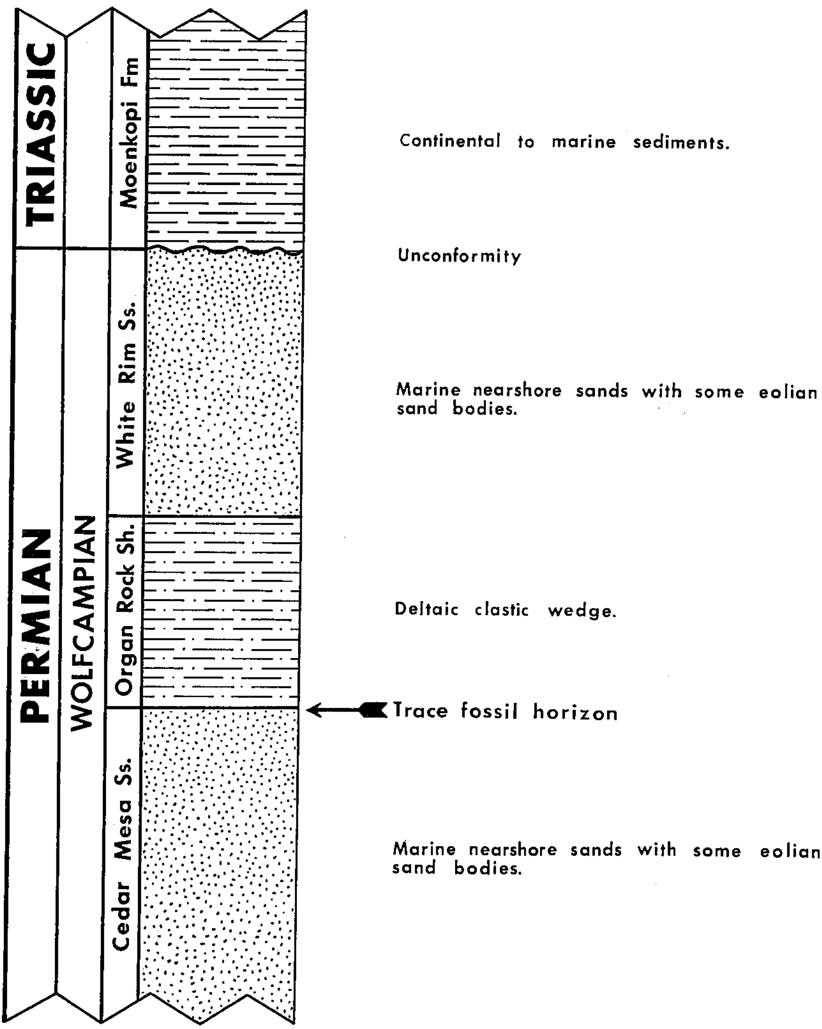
Ophiomorpha nodosa Lundgren and *Ardelia socialia* n. ichngn.-sp. occur at several places in the top of the Cedar Mesa Sandstone, beginning a few miles northeast of Hite, Utah, and continuing for approximately 30 miles northeast to Teapot Rock near Elaterite Basin on the northwest side of the Colorado River part of Cataract Canyon (Text-fig. 1).



TEXT-FIGURE 1.—Index to the localities of the trace fossils *Ophiomorpha nodosa* Lundgren and *Ardelia socialia* n. ichngn.-sp. from the Wolfcampian-Leonardian (?) Cedar Mesa Sandstone of the Colorado Plateau, Utah.

STRATIGRAPHY

The Cedar Mesa Sandstone of the Cataract Canyon ranges in thickness from approximately 1,200 feet in the southwest to 600 feet in the northeast and is Wolfcampian in age (Baars, 1961, 1962) and possibly Leonardian in the upper part (Irwin, 1971). It overlies the red beds of the Halgaito Shale and underlies the red beds of the Organ Rock Shale (Text-fig. 2). Ten to 40 miles to the east of Cataract Canyon, the Cedar Mesa undergoes a rapid facies change to the red shales, siltstones, arkoses, anhydrite lenses, and fine-grained red sandstones of the lower Cutler Formation. Approximately 80 miles northwest it



TEXT-FIGURE 2.—Stratigraphic position of *Ophiomorpha nodosa* Lundgren and *Ardelia socialia* n. ichngn.-sp. and general Permotriassic stratigraphy in Cataract Canyon, Utah.

merges with the White Rim Sandstone member of the Toroweap Formation (Irwin, 1971).

The Cedar Mesa Sandstone is a white to light gray, highly calcareous quartzose sandstone. The grains are fine to medium, well rounded to subangular, and well sorted. Baars (1961, 1962) stated that the sands were derived from the northwest and were deposited by persistent currents to the southeast in nearshore, shore, and tidal-flat environments.

Baars (1961, 1962) and Irwin (1971) provide further details on biostratigraphy, stratigraphy, sedimentary petrology, and paleogeography.

BURROWS AND FOSSORIAL SHRIMP

Geologic range of thalassinid burrows.—The Jurassic-Cretaceous speciation of thalassinid and other decapods is accompanied by a diversification in types of thalassinid burrows. Text-figure 3 depicts the geologic range of several important burrows and the geologic range of some decapods thought responsible for them. On the basis of burrow geometry, nodose wall structures, fossil shrimp or fecal pellets within the burrows, and/or continuation of one type of burrow into another type, these burrows are all thought to have been made by closely related decapods, probably fossorial shrimp.

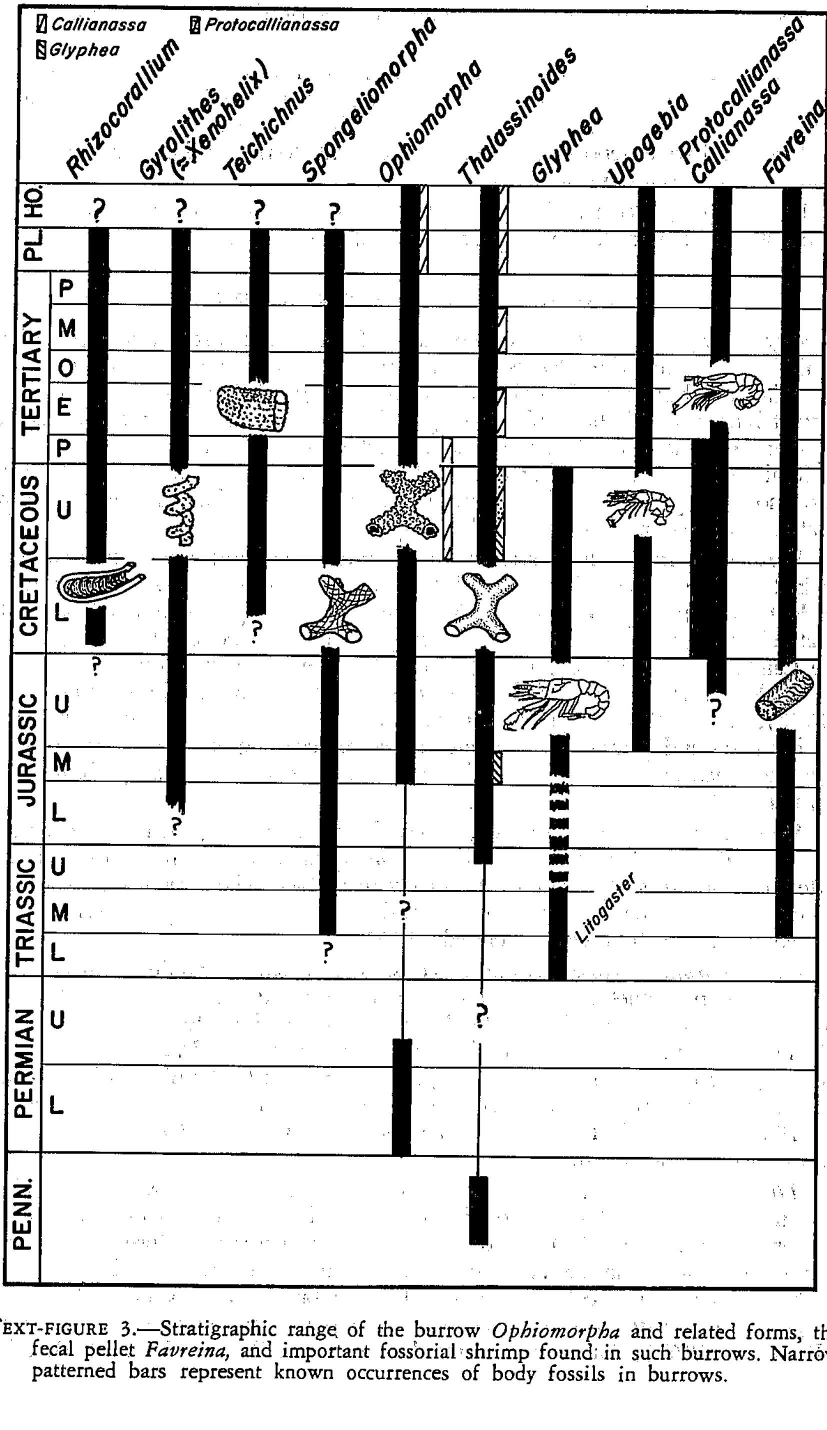
Rhizocorallium with relatively large outer tubes and wide spreiten and packed with small rod-shaped fecal pellets similar to *Favreina* were probably made by decapod crustaceans, perhaps fossorial shrimp. *Rhizocorallium* with relatively narrow outer tubes and narrow spreiten and without pellets range from the Cambrian to the Holocene and probably were made by worms.

Nodose forms of *Gyrolithes* (*Xenohelix*) described by Hestor and Pryor (1972), Keij (1965), and Stanton and Warme (1971) result from a particular behavior and physiology and are therefore regarded as being variations of *Ophiomorpha,* as are the nodose forms of *Teichichnus* reported by Hestor and Pryor (1972).

Spongeliomorpha is a striated, grooved, and branching burrow. Its geometry is similar to *Thalassinoides* and *Ophiomorpha,* and some forms of both the latter have striate sculpture on the inner wall surface. The scratch marks are attributed to continual scraping of the walls by crustacean appendages as they moved against the tube wall (Kennedy, 1967).

Ophiomorpha nodosa Lundgren consists of a smooth-walled central tube, 1 to 2 cm in diameter, with a collophanite-cemented wall (Land *in* Weimer and Hoyt, 1964; cf. Smith, 1967) that is nodose on the exterior. Kennedy and MacDougall (1969) considered the thick, striated rods of *Halymenites striatus* Lesquereux to represent the filling of galleries and shafts of callianassid burrows and thus considered the rods a form of *Ophiomorpha. Scoyenia gracilis* White (1929) from the Hermit Shale of Arizona is very similar to *H. striatus* and may be a junior synonym.

Thalassinoides is usually a smooth-surfaced branching burrow that branches at a more-or-less constant angle of 120°. It has been traced into *Ophiomorpha* (Ager and Wallace, 1970), and some forms are slightly nodose. In such instances it is clear that *Thalassinoides* was made by a callianassid, but *Glyphea* (Glypheoidea) has also been found within this burrow (Sellwood, 1971). The range of *Thalassinoides* was regarded as Upper Triassic through Holocene (Kennedy, 1967), but certain irregular forms similar to those of Bromley



TEXT-FIGURE 3.—Stratigraphic range of the burrow *Ophiomorpha* and related forms, the fecal pellet *Favreina*, and important fossorial shrimp found in such burrows. Narrow patterned bars represent known occurrences of body fossils in burrows.

(1968) are known from the upper Pennsylvanian of Texas (Warme and Olson, 1971, figs. 27, 28) and burrows similar to those made by *Upogebia* or *Callianassa californiensis* Dana are known from the Desmoinesian part of the Oquirrh Formation of Utah (Chamberlain and Clark, 1973, in press).

Favreina is a distinctive fecal pellet that has been shown to be made by reptant decapods (Kennedy, Jakobson, and Johnson, 1969). *Favreina* has been found in the burrow *Thalassinoides* associated with *Callianassa* of Miocene age (Ehrenberg, 1944), in the burrow *Thalassinoides* associated with three brachyurans of Jurassic age (Kennedy, Jakobson, and Johnson, 1969), in the burrow *Ophiomorpha* of Upper Cretaceous age (Brown, 1939), and in *Thalassinoides* containing Middle Jurassic *Glyphea* (Sellwood, 1971).

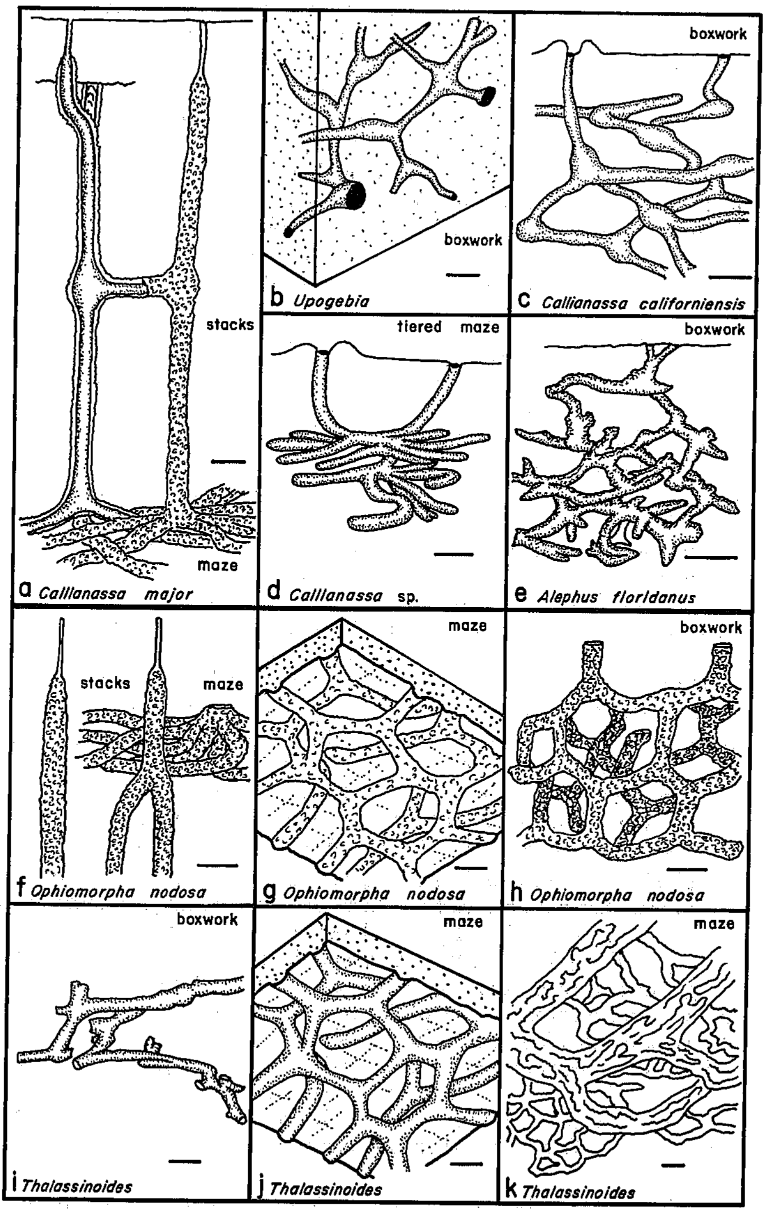
Basic thalassinid structures.—In a further attempt to determine the most probable relationships of the Cedar Mesa *Ophiomorpha nodosa* and *Ardelia socialia* n. ichngn.-sp. to other thalassinid burrows, the several aspects of *Ophiomorpha* and *Thalassinoides* and of the burrows of some extant shrimp were reviewed. As depicted in Text-figure 4, these forms can be categorized as "stack," "maze," and/or "boxwork" structures.

The classical burrow of *Callianassa major* (Text-fig. 4a) consists of five components, which are, from top down, (1) a narrow tube ranging from 10 to 30 cm in height and from 3 to 5 mm in diameter and extending to the surface, (2) a widening neck, (3) a relatively wide vertical stack (1 to 2 cm across outside of walls) made of a central tube with a smooth inner surface and a wide mucus-cemented wall with a nodose exterior and a height ranging from 1 to 4 meters, (4) horizontal crossties between stacks, and (5) a horizontal, radiating, and branching maze at the bottom of the stack (Weimer and Hoyt, 1964; Frey and Mayou, 1971; Pohl, 1946; cf. *C. trilibata* Biffar, 1971).

Upogebia (Callianassidae) builds a limited ramifying boxwork (Text-fig. 4b). It is a suspension feeder and does not need to add new galleries continually —as do many other fossorial shrimp (MacGinitie, 1930). The burrows of *Callianassa* sp. described by Shinn (1968) consists of two or more levels of radiating tubes that may be described as "tiered-maze" (Text-fig. 4d).

Classical *Ophiomorpha nodosa* Lundgren are identical to burrows built by *Callianassa major* Say with the vertical stacks and lower radiating maze all showing the nodose exterior (Text-fig. 4f; Hoyt and Weimer, 1965; Hestor and Pryor, 1972; Keij, 1965; Pickett, Kraft, and Smith, 1971). Extensive nodose mazes (e.g., Dakota Sandstone of northwestern New Mexico) and boxworks (e.g., Warme and Stanton, 1971) of *O. nodosa* that show typical 120° branching and that are essentially independent of stacks are common in the geologic record of the Cretaceous and the Tertiary (Text-fig. 4g, h). Boxwork forms of *Thalassinoides* (Text-fig. 4i; Kennedy, 1967; Frey, 1970b) and maze forms (Text-fig. 4j, k; Howard, 1966; Frey and Howard, 1970; Frey, 1970b; Scholz, 1968; Bromley, 1968) are essentially smooth tubes branching at the characteristic 120°.

The nodose, tubular burrows from the Permian Cedar Mesa Sandstone are sufficiently similar (even identical) to *Ophiomorpha nodosa,* to warrant calling them *O. nodosa* also. Burrows identical to *Ardelia socialia* n. ichngn.-sp. from the Cedar Mesa have not been found. The burrow of *Callianassa* sp. (Shinn, 1968) is similar to *Ardelia,* and if the dense branching were repeated and extended over greater distances, an identical burrow might result.



TEXT-FIGURE 4.—Representative burrows of extant Thalassinoidea (a-e) and structure of various trace fossils attributed to the Thalassinoidea (f-k). Fig. *b* from Hertweck and Reineck, 1966; fig. *c* modified from MacGinitie, 1934; figs. *d* and *e* from Shinn, 1968; fig. *i* from Kennedy, 1967; fig. *j* from Kemper, 1968, 1969, and Howard, 1966; and fig. *k* from Bromley, 1968. Bar scales all 5 cm.

Ecology and paleoecology.—Weimer and Hoyt (1964) showed *Callianassa major* Say at Sapelo Island to be most common in the littoral zone. Frey and Mayou (1971) found *C. major* to be less dense in the upper foreshore of Sapelo Island and most dense in the lower foreshore; the latter forms had crossties between the vertical stacks. *C. major* has also been reported on sandy tidal flats and shoals (Frey, 1970a) and in tidal-stream bars in salt marshes (Frey and Howard, 1969). At approximately 1 m water depth other species of *Callianassa* replace *C. major* in the shoreface (Frey and Mayou, 1971).

Callianassa sp. (Shinn, 1968) was profuse in the intertidal zone of the Bahamas and Florida. *Callianassa californiensis* Dana of Mugu Lagoon as described by Warme (1967) occurs mostly in the intertidal and subtidal zones. MacGinitie (1934) reported this species from sandy mud bottoms in estuaries and bays of the west coast of North America ranging from zero to plus one foot in the intertidal zone. Biffar (1971) described several species of *Callianassa* from south Florida and made some short notes on their habitat and burrow morphology. Most are bay, lagoon, or estuary forms building what are probably boxwork burrows.

Ophiomorpha described by Hillmer (1963) and Keij (1965) were thought to have been constructed in freshwater and brackish-water environments, respectively. Howard (1972, oral communication to Chamberlain) has noted that boxwork *Ophiomorpha* are indicative of lagoon or bay areas. Warme and Stanton (1971) found boxwork *Ophiomorpha* in a probable intertidal crevasse-splay deposit in the Tertiary of Texas. *O. nodosa* and *Ardelia socialia* n. ichngn.-sp. from the Cedar Mesa Sandstone are boxwork forms and are probably excellent examples of tidal-flat forms.

TRACE-FOSSIL DESCRIPTIONS

Genus OPHIOMORPHA Lundgren, 1891
OPHIOMORPHA NODOSA Lundgren, 1891

Text-figs. 3, 4a, f-h; Pl. 3, figs. 4-8.

Ophiomorpha nodosa Lundgren, 1891, p. 114-115, figs. 1-2; Kennedy and MacDougall, 1969, p. 459-471, pls. 87-88, fig. 1 (see for extensive synonymy); Hestor and Pryor, 1972, p. 677-688, fig. 3.

"burrows of a callianassid crustacean" Pickett, Kraft, and Smith, 1971, p. 209-211, pl. 28, fig. 2.

Ophiomorpha Howard, 1966, p. 46, fig. 11; Heinberg, 1970, p. 233; Baer, 1971, p. 366; Warme and Stanton, 1971, p. 11-15; Hestor and Pryor, 1972, p. 677-688.

Ophiomorpha sp. "A" Frey and Howard, 1970, p. 163, fig. 7d.

Description.—Vertical and horizontal sandstone pipes, 20-40 mm in diameter and greater than 60 mm long. Generally straight but can be curving. Wall approximately 7 mm thick, shaft in center 10-20 mm in diameter. External surface nodose; nodes average 3 mm across.

Remarks.—Additional *Ophiomorpha nodosa* have been found in the lower 70 feet of the Upper Jurassic Curtis Formation in Finch Draw, five miles east of Highway 44 near the shores of Flaming Gorge Reservoir. This location is on the north slope of the Uinta Mountains, Daggett County, Utah. The burrows occur in glauconitic, arenaceous, silty units. They were collected by Roger D. Hoggan in what he interpreted to be an upper neritic to subtidal environment (written and oral communication, 1970). Hoggan's specimens are in the Brigham Young University Paleontology Collections.

Ichnogenus ARDELIA n. ichngn.
ARDELIA SOCIALIA n. ichnsp.

Text-fig. 5; Pl. 1, figs. 1-7; Pl. 2, figs. 1-5; Pl. 3, figs. 1-3.

Description.—Large horizontal sandstone cylinders and rods joined by vertical and/or oblique ones. Surface relatively smooth on most horizontal forms but varies to moderately or highly irregular and nodose, particularly on inclined forms. May be straight or curving. Diameters of the total structure range from 10 to 20 cm; lengths, from 30 cm to over 2 meters. These large structures are actually made up of profuse radial bifurcations from central galleries. These secondary galleries are 3 to 7 cm across, and some protrude 10 cm.

No wall lining apparent, but diagenetic iron in and near the burrows varies from moderate to extreme concentrations and tends to outline the central gallery and radiating tubes, which are not affected much.

Remarks.—This intense and extensive bioturbation implies very active working of the sediment by perhaps more than one individual. The generic name *Ardelia* denotes the intense activity and reworking of the sediment. The specific name *socialia* alludes to the possible communal association.

Lee F. Braithwaite, of the Brigham Young University Zoology Department (oral communication to Baer, 1971), thought that these structures were perhaps due in a great degree to "housecleaning," the stuffing of fecal material into the walls by an animal such as *Upogebia*. It seems that even in this situation much mining activity would be required to provide so much space and material for the extensive "stuffing."

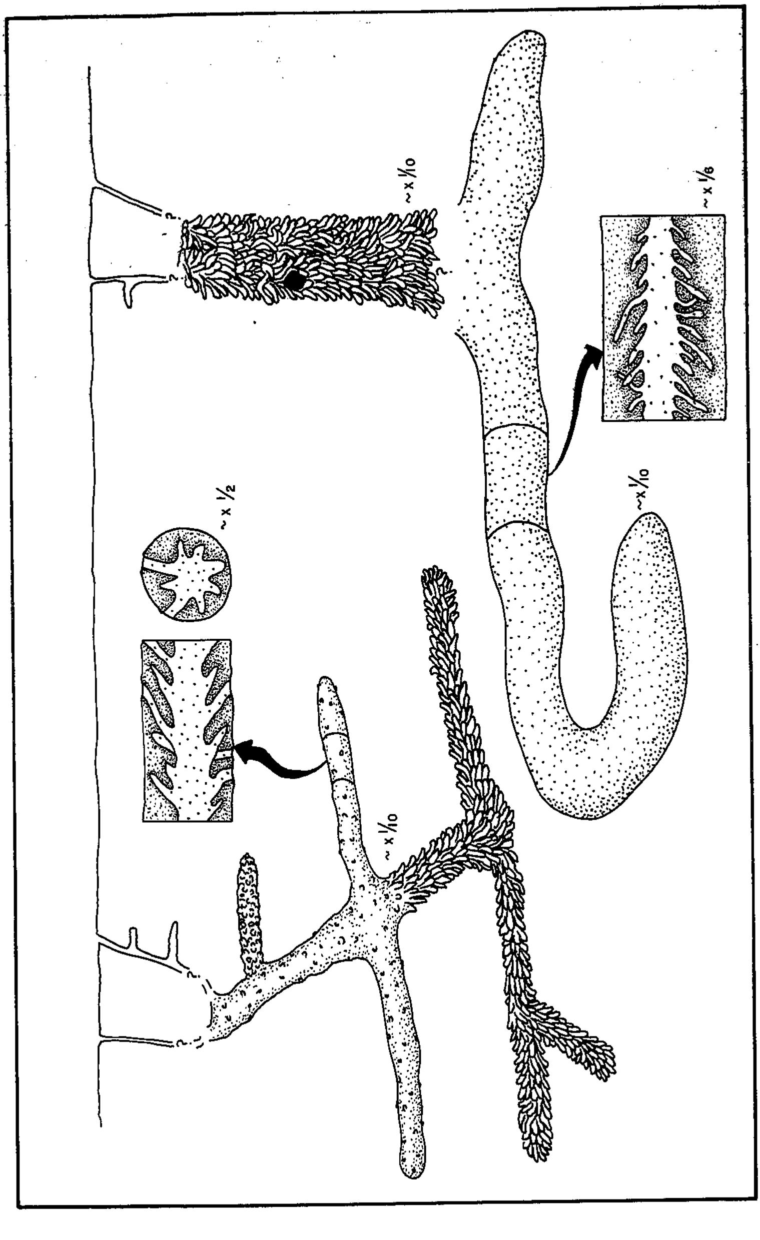
Repository.—Specimens illustrated in this paper are on deposit in the Brigham Young University Paleontology Collections and bear the numbers BYU #1963-1972. The ichnotype species of *Ardelia socialia* is BYU #1965.

CONCLUSIONS

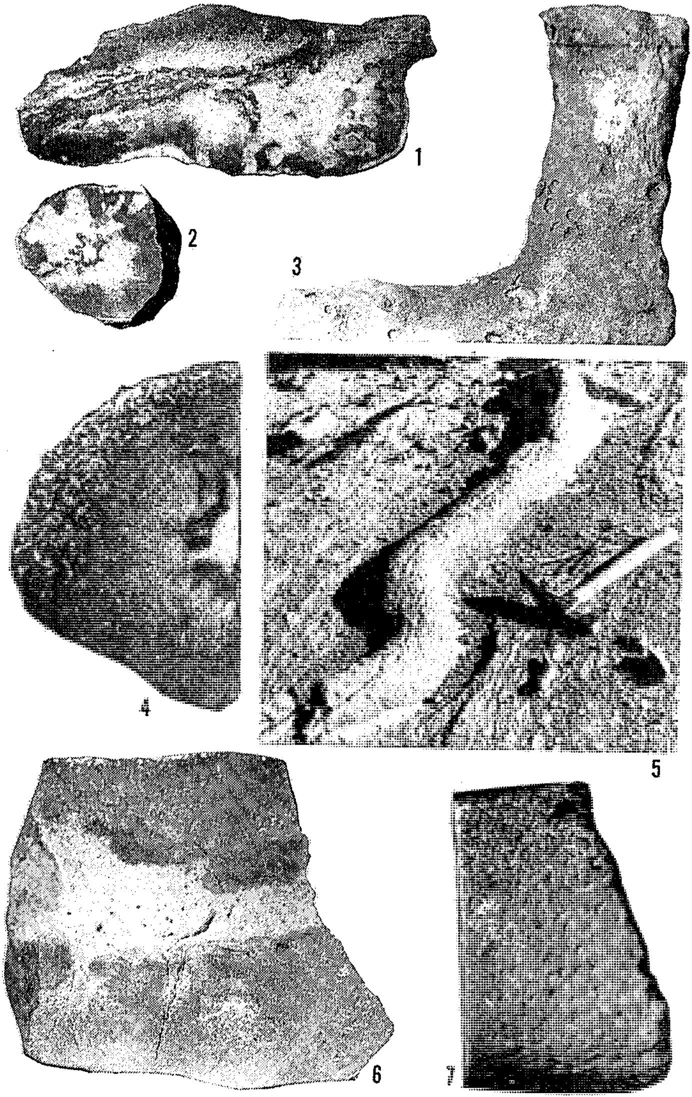
Ophiomorpha nodosa Lundgren and *Ardelia socialia* n. ichngn.-sp. from the Wolfcampian Cedar Mesa Sandstone of Utah are thalassinid burrows that predate the earliest report of fossil decapods.

The discrepancies between the early occurrence of thalassinid burrows in the Permian and the later occurrence of thalassinid body fossils may be resolved if more body fossils are found to provide additional information on the origin and development of the decapods, particularly of the thalassinid line.

It is not unusual for related animals like the Glypheoidea and Thalassinoidea to develop similar simple branching feeding burrows such as *Thalassinoides*. It is less likely that both would develop the more specialized habit of firming up the burrow wall with collophanite-cemented sand pellets such as is done in *Ophiomorpha* burrows known to be made today by *Callianassa major* Say. As it stands now, the early occurrence of Permian *Ophiomorpha* provides evidence for early development of the Thalassinoidea.



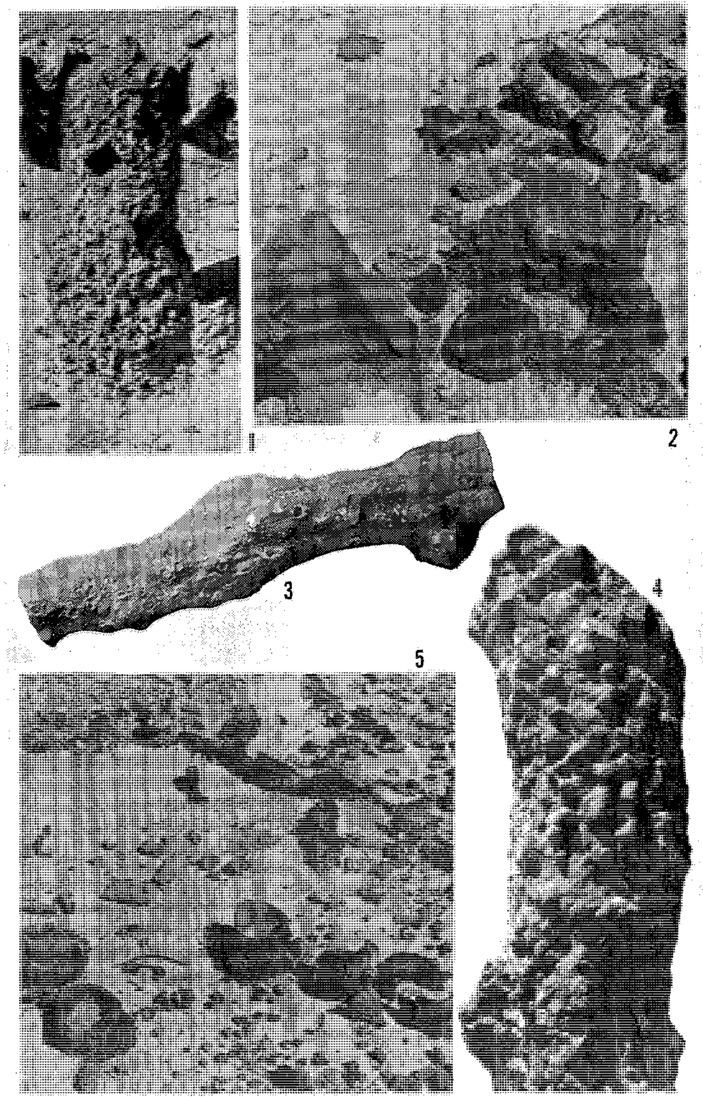
TEXT-FIGURE 5.—Composite reconstruction of *Ardelia socialia* n. ichngn.-sp. from the Wolfcampian-Leonardian (?) Cedar Mesa Sandstone of Cataract Canyon, Utah. Fine stipple on enlarged, cutaway-insets represents increased diagenetic iron concentration towards central gallery and radiating tubes. Small access tubes at top of structures conjectural.



EXPLANATION OF PLATE 1

Figs. 1-7.—*Ardelia socialia* n. ichngn.-sp.

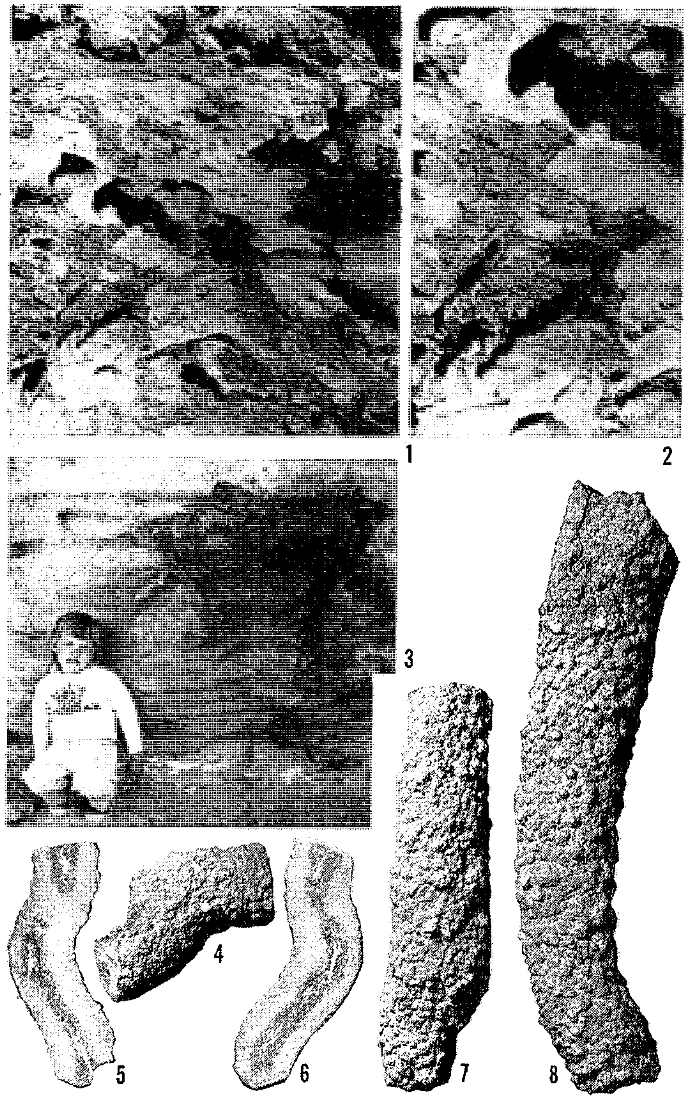
1. Longitudinal view of slab off ichnotype species to show small tubes branching off core tube. 3/5 X, BYU #1963. *2.* Transverse view of slab from ichnotype species, showing small tubes radiating from core galley. 3/5 X, BYU #1964. *3.* Ichnotype species. Top view; note pits that correspond to tubes. 3/5 X, BYU #1965. *4.* Transverse view of slab from large specimen. Note central region with radiating tubes and note progressive decrease in concentration of diagenetic iron oxides from center towards upper left of structure. ½ X, BYU #1966a. *5.* Perspective view of outcrop, illustrating typical large form. *6.* Longitudinal view of slab from large specimen, also showing light-colored sand core and branching tubes. ½ X, BYU #1966b. *7.* Surface of large specimen shown in fig. 4, illustrating nodose structure attributed mainly to diagenetic concentration of iron oxides. ½ X, BYU #1966a.



EXPLANATION OF PLATE 2

Figs. 1-5.—*Ardelia socialia* n. ichngn.-sp.

1. Large vertical form built of numerous small tubes radiating outward. Approximately 1/8 X. *2*. Large vertical forms that show the diagenetic concentration of iron oxides in a wide rind and a thick, easily weathered, slightly affected core. *3*. Medium-sized, inclined form that shows smaller tubes through diagenetic rind. 1/3 X, BYU #1967. *4*. Medium, inclined form that shows strong nodose surface attributed to radial probing by deposit feeding animal. 2/5 X, BYU #1968. *5*. Large vertical forms, showing the strong diagenetic concentration of iron oxides in thick rind and easily weathered, slightly affected core. Note medium-sized, nodose form in upper right essentially horizontal to bedding.



EXPLANATION OF PLATE 3

Figs. 1-3.—*Ardelia socialia* n. ichngn.-sp.

1, 2. Inclined medium forms, showing the numerous sandfilled tubes that make up the larger structures. 1/16 X and 1/8 X, respectively. *3.* Large horizontal and vertical forms, showing extensive vertical development of burrowing system. From Cedar Mesa Sandstone of Cataract Canyon, Utah.

Figs. 4-8.—*Ophiomorpha nodosa* Lundgren.

4, 7, 8. Permian forms of *Ophiomorpha* from the Wolfcampian Cedar Mesa Sandstone of the Colorado Plateau, Utah, showing typical nodose exterior. ½ X, BYU #1969-71, respectively. *5, 6.* Sawed specimen, showing central tube. ½ X, BYU #1972a and b, respectively.

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