

Endobenthic adaptations of juvenile thalassinidean shrimp

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A burrow of *Upogebia affinis* observed near Sapelo Island, Georgia, includes two enlarged chambers bearing numerous minute tunnels that branch in characteristic thalassinoid pattern. The latter are interpreted as excavations made by young postlarvae of *U. affinis*. Examples of this phenomenon have been recorded for *Callianassa kraussi* in South Africa, and possible trace fossil analogs have been observed in the Pleistocene of North Carolina and the Permian and Cretaceous of Utah.

In other casts of *Upogebia affinis* burrows, some components vary considerably in diameter and interconnect with the main burrow system by means of branches that have constricted apertures. These variable burrows evidently represent a growth sequence, from domiciles excavated by small juveniles to those of normal adults.

We also speculate that certain shrimp species may utilize plant debris for the culture of edible microorganisms within the burrow.

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Reconnaissance studies of burrowing marine organisms near Sapelo Island, Georgia (Mayou, Howard & Smith 1968; Frey & Howard 1969), yielded a polyester resin cast of an unusual burrow system of the thalassinidean shrimp *Upogebia affinis*. The system had two enlarged terminal chambers (fig. 1), from which peculiar clusters of tiny burrows protruded (fig. 2).

The minute structures were intriguing but difficult to explain. They could be interpreted either as burrows of juvenile *Upogebia affinis*, or as independent burrows excavated by a commensal of the shrimp or by a subsequent inhabitant of the shrimp burrow. We preferred the first interpretation; the tiny burrows closely resembled the large burrows of adult *U. affinis* (fig. 3A). The specimens conjured up images of a 'hatching structure' [term used in the sense of 'Brutbauten' (Seilacher 1953 p. 434)] of some sort, comparable to that suggested for certain branched dwelling tubes of the anemone *Ceriantheopsis americanus* (Cutress, in Frey 1970 a, p. 309-310). Yet the literature on *Upogebia affinis*, including the older papers cited by Williams (1965) and the recent work by Sandifer (1973, 1974), in-

dicates that the larvae are planktic and therefore would not be expected to remain inside the parent burrow during ontogeny.

Burrows of the phoronid *Phoronis pallida* have been observed in commensal interrelationship with the burrows of *Upogebia pugetensis* in Bodega Bay, California (Thompson 1972). But we could not discover the identity of the presumed secondary burrower associated with *U. affinis*; the tiny structures simply did not resemble the burrows of any polychaetes (e. g. fig. 2A) or other small animals known to us.

We dismissed the third possibility, burrowing by a subsequent inhabitant of the shrimp domicile, because the burrow bore all signs of active occupation by *Upogebia affinis*.

Then our attention was drawn to the work of Forbes (1973) who, in estuaries near Port Elizabeth, South Africa, reported examples of juvenile shrimp burrows radiating off the parent burrows of *Callianassa kraussi*. Our specimen is similar in many respects to that pictured and described by Forbes (1973, fig. 4), and seems to have originated essentially in the same way. The major difference between the two apparently is that larvae of *C. kraussi*

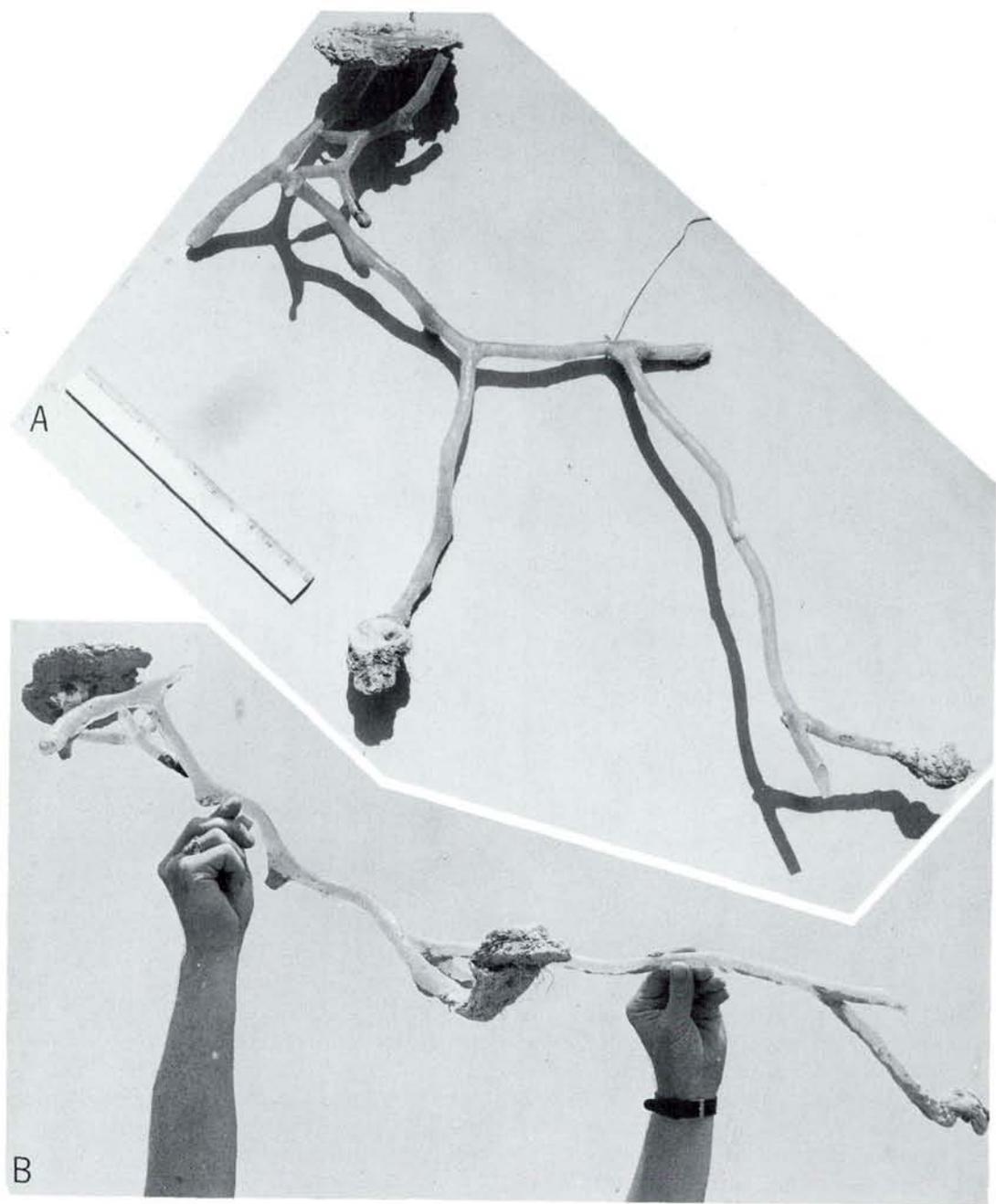


Fig. 1. Polyester resin cast of burrow of the modern thalassinidean shrimp *Upogebia affinis*, illustrating enlarged terminal chambers from which tiny burrows extend (see fig. 2). A, oblique view; a burrow of intermediate size interconnects with the larger host burrow near the top; this slightly smaller burrow exhibits a typical thalassinoid branching pattern and

dead-end tunnel, but joins the main burrow via two highly constricted necks (seen better in the shadow). Scale (ruler) 30.5 cm. B, side view, showing inclined components and lateral extent of the burrow; the cast was broken in places during recovery. From muddy estuarine point-bar sediments; Sapelo Island, Georgia.

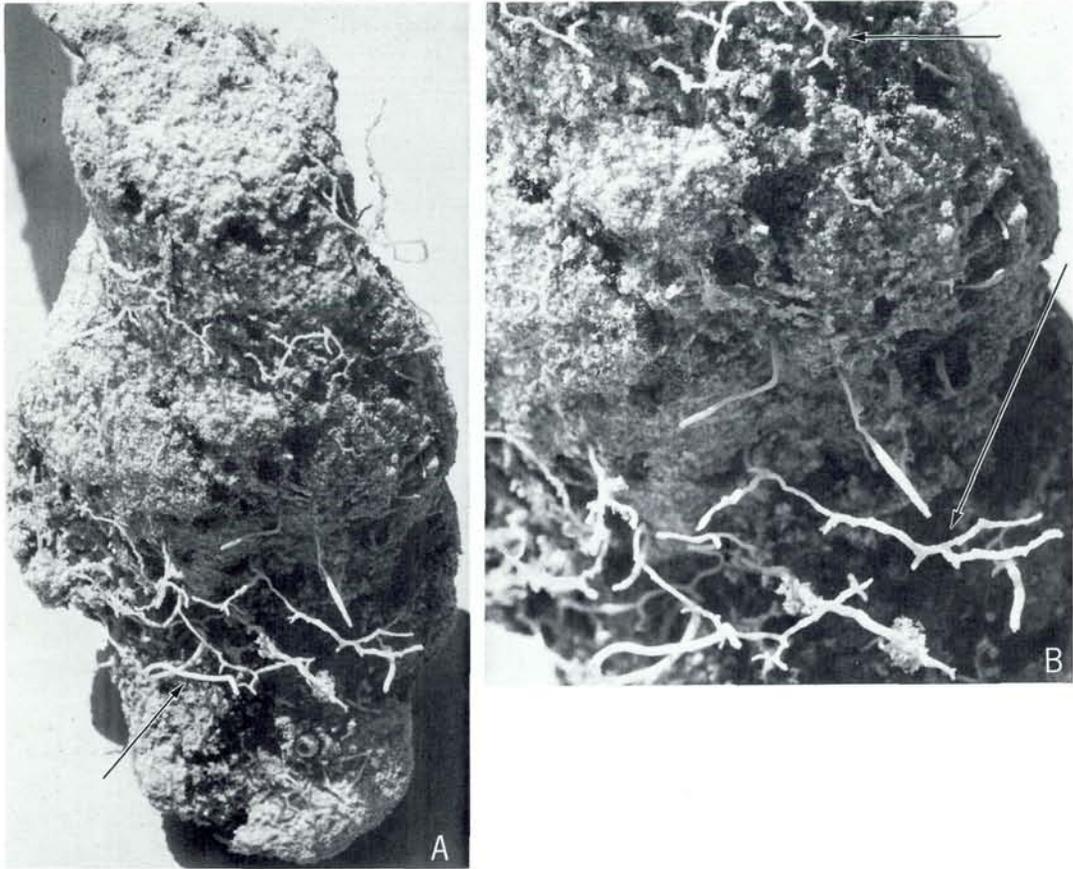


Fig. 2. Enlargements of one of the chambers shown in fig. 1 (center), illustrating clusters of tiny burrows. A, upper surface of chamber; smooth sinuous burrow of a polychaete indicated by arrow. B, enlargement

of small burrows; those exhibiting especially well developed thalassinoid characteristics are indicated by arrows (cf. fig. 3A).

never leave the parent burrow whereas those of *Upogebia affinis* undergo a normal planktic stage; after metamorphosis, some postlarvae of *U. affinis* evidently reenter the burrows of adults rather than settling directly upon the substrate surface, to establish their initial domiciles.

Organic matter contained in the enlarged chambers of the *Upogebia affinis* burrow, together with that observed in burrows of other species, also makes us wonder whether various shrimp may utilize cultures of bacteria for food, possibly for infaunal offspring as well as for themselves.

The ecologic and ethologic importance of such 'unusual' adaptations is evident, and the

ichnologic expression of much of this behavior is capable of being preserved in the fossil record. Possible fossil analogs have indeed been found, as discussed below. Numerous other examples, both recent and ancient, may eventually be discovered (cf. Kern & Warne 1974, fig. 7a; Ginsburg & Hardie 1975, fig. 4b).

Many of our discussions here are intentionally speculative, and the ideas expressed will need further testing. Our main goal is to call specific attention to various little-known but evidently very important variations among thalassinideans and similar shrimps, and to encourage further study of them.

Natural history of *Upogebia affinis*

Upogebia affinis ranges geographically from Massachusetts to Texas, the West Indies, and Brazil, and bathymetrically from the lower intertidal zone to depths of 30 m (Williams 1965). The shrimp inhabits muddy estuarine or nearshore sediments, in places where salinities are moderately high (typically 25–30 ‰, although less in some places) and gentle waves or tidal currents keep the waters well circulated. Burrows are excavated both in bare substrates (Frey 1970 b, pl. 90, fig. 1) and in sediments stabilized by marine grasses (Wass 1955); most such substrates are highly reduced, yet burrow interiors are kept well oxygenated by water circulating through the burrow system.

Burrows of *Upogebia affinis* are abundant in, and characteristic of, the muddy estuarine sediments of coastal Georgia, and have been studied there in some detail (Smith 1967; Frey & Howard 1969; Howard & Frey 1973, 1975 b). The interconnected burrows penetrate irregularly into the substrate to depths of 50 cm or more, and some extend laterally for distances of at least 2 m. The overall burrow system presumably extends over much greater lateral distances. [If numerous burrows in a given population are interconnected, as they seem to be, then these essentially form one large communal structure. But large three-dimensional burrow systems such as these are difficult to cast and recover; air or water locks frequently block the flow of the resin, and even when penetration is good, the large intricate casts are fragile and difficult to excavate intact – e.g., broken tunnels are evident in fig. 1.] In the sense of Chamberlain & Baer (1973, text-fig. 4) and Bromley & Frey (1974), the configuration of the burrow system is mainly that of a ‘box-work.’

The burrows are typically enlarged at points of bifurcation and have Y-shaped branches, swollen ‘turn-arounds’, and blind tunnels (fig. 3 A). At and just below the substrate surface the burrows are conspicuously constricted, much like the aperture of burrows of *Callianassa major* (Frey & Howard 1972, fig. 6), *C. kraussi* (Forbes 1973), and *Upogebia pugettensis* (Thompson 1972). This constricted pas-

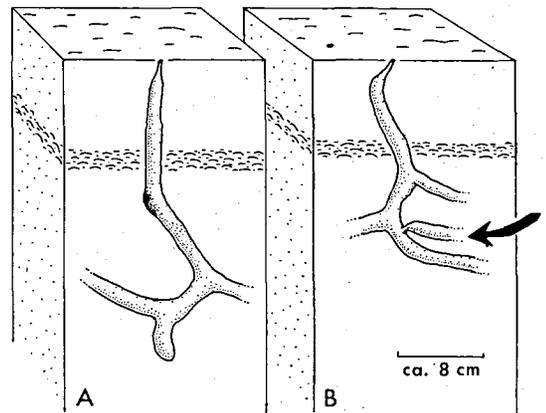


Fig. 3. Typical burrows of *Upogebia affinis*. A, specimen illustrating characteristic apertural neck, Y-shaped branches, ‘turn-around’, and blind tunnel. B, similar specimen, but bearing a branch (arrow) in which the connection with the main shaft is constricted, like an apertural neck. Sketched from resin burrow casts; Sapelo Island, Georgia.

sage, 2–5 cm long in typical burrows of *U. affinis*, was informally termed ‘section A’ by Smith (1967) and has been called the ‘A-tube’ by others; here we refer to it as the ‘apertural neck.’ Comparable constrictions are also found occasionally at points of branching within the burrow system (fig. 3 B), as explained below.

The lined walls of *Upogebia affinis* burrows, although relatively thin in most Georgia estuarine specimens, are smooth and durable. Thicker walls consist of two discernible layers much like those of *U. pugettensis* (Thompson 1972): a smooth mucoid inner layer and a more particulate outer layer. Smith (1967) reported a pelletoidal burrow exterior, evidently somewhat resembling that of *U. pugettensis* (Thompson 1972) or *Callianassa major* (Weimer & Hoyt 1964). Yet these knobby walls have not been observed elsewhere among burrows of *Upogebia affinis*.

Burrows of presumed juvenile *Upogebia affinis*

The communal burrows of *Upogebia affinis* commonly contain ovigerous females and juveniles (Pearse 1945), although no one seems to have observed individuals of the

early postlarval stage within the parent domicile. The tiny burrows cast by us, about 1 mm in diameter and as much as 3 cm long, are of the proper magnitude and configuration to be postlarval excavations (cf. Forbes 1973). Our main evidence for this interpretation is the close similarity between the tiny burrows and the larger ones of adult *Upogebia affinis* (figs 1-3). The small burrows, in mimicry of the big ones, are highly ramified and exhibit notable Y-branches, blind tunnels, "turn-arounds," and occasional constricted branches. Apertural necks are not conspicuous where the tiny structures join the host chamber, but they may have been masked somewhat by seepage of the resin through the irregular wall layering there. The burrows themselves are smoothly lined and well constructed, as demonstrated by the cast.

In addition, several casts of interconnected *Upogebia affinis* burrows observed by us exhibit branches that are constricted, rather than being enlarged, at points of bifurcation (figs 1A, 3B, 4). These constrictions are reminiscent of surface openings of the larger burrows and support our contention that the branches were formed by postlarvae burrowing from within the domicile of an adult shrimp rather than from the substrate surface. The connections remain open but obviously are too small to permit the passage of large shrimp. Possibly these constricted branches are related to hydrodynamics, a valvelike device to enhance the efficiency with which water can be pumped through given parts of the burrow system. But adult shrimp observed by us in aquaria do not construct such branches, and neither does this explain the satellite burrows lacking a connection with the substrate surface (fig. 4). Thus, the constrictions more likely represent relict apertural necks or original juvenile shrimp burrows still connected to the host burrow.

In this regard, the behavior of *Upogebia affinis* therefore differs from that of *Callinassa kraussi*. The latter, as adults, completely abandon the original part of their postlarval excavation (Forbes 1973), whereas in the adult stages of *Upogebia affinis* these apertural necks are evidently reformed into

the typically enlarged branches of 'normal' thalassinoid burrows.

The constricted branches are best developed where associated with burrow components of different sizes. In numerous specimens the shafts and tunnels stemming from the constricted branches are smaller in diameter than the host shafts and tunnels (fig. 4). In other specimens the two sets of burrows may be only slightly different (fig. 1A) or essentially the same size (fig. 3B). We interpret these differences in diameter as a reflection of the growth of the individual shrimp, an ontogenetic sequence represented by the burrows. Thompson (1972) found an almost linear relationship between the length of the carapace and the diameter of the burrow of *Upogebia pugettensis*.

The configuration of the smaller burrows shown in fig. 4 indicates that the juveniles' burrows can originate at various different places along the shafts and tunnels of adult shrimp burrows and are not confined to definite 'pouches' such as those shown in figs 1 & 2.

Plant debris in shrimp burrows

The filter and deposit feeding activities of many thalassinideans are generally well known (e. g., MacGinitie & MacGinitie 1968; Schäfer 1972). But plant matter found in wall linings and special chambers of various shrimp burrows suggests that other specialized feeding behaviors may exist.

The walls of the bulbous enlargements of the *Upogebia affinis* burrows, as well as occasional blind tunnels and pockets, are irregular and comparatively ill maintained. Here the lining consists not only of agglutinated clayey sediments but also of particulate organic matter. Although not easily identifiable, this matter may be finely fragmented plant debris, possibly derived from the grass *Spartina* in adjacent salt marshes (cf. Odum & de la Cruz 1967). This grass is tremendously important in the trophic structure of Georgia estuarine and nearshore communities (Howard & Frey 1975a) and conceivably may be utilized by

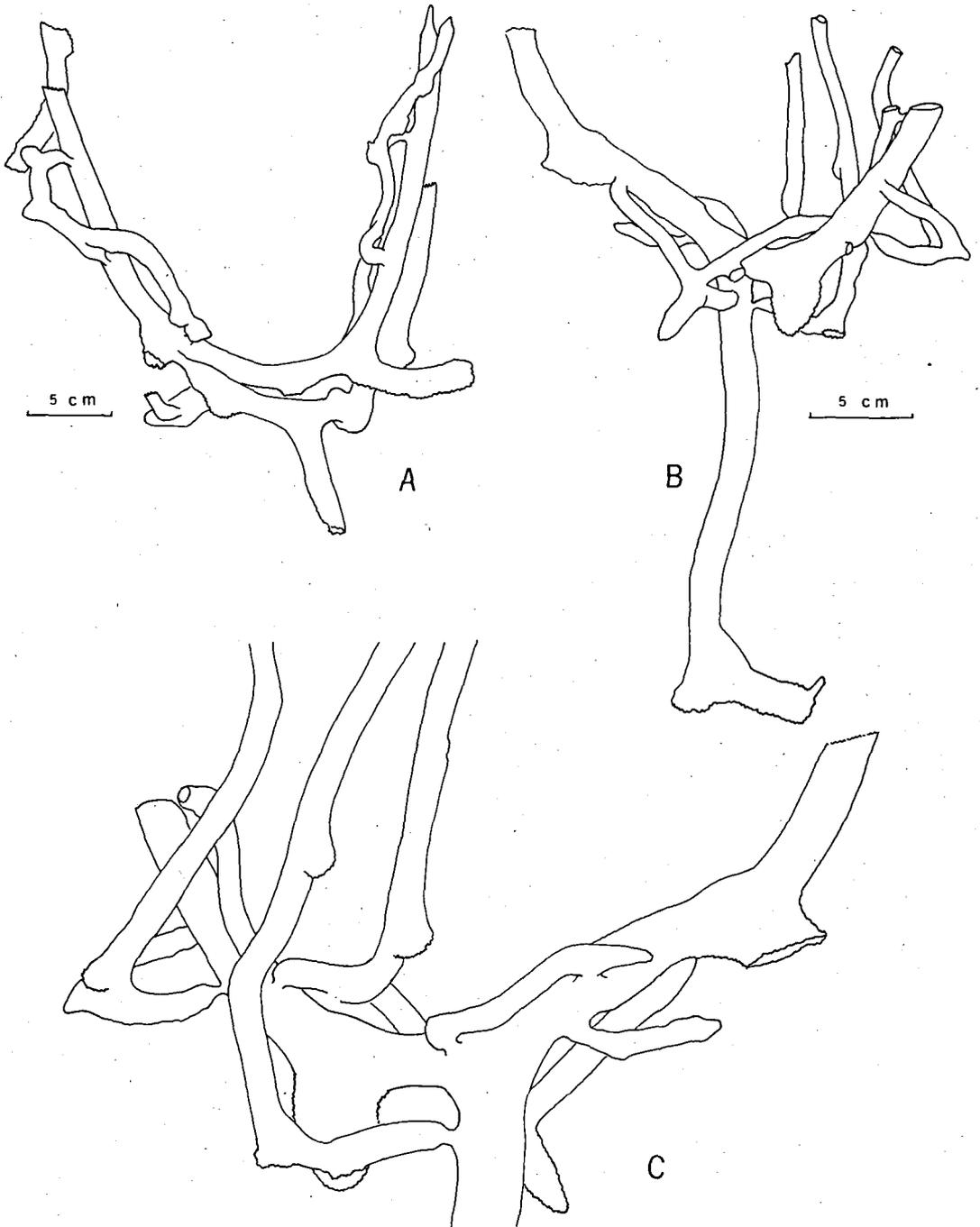


Fig. 4. Interconnected burrows of *Upogebia affinis*, showing variations in diameter and configuration of components. Lateral views. Most burrows were connected with the substrate surface, but some of the smaller satellite burrows were not; virtually all have

constricted necks. A, an overall Y-shaped burrow system. B, a more irregular Y-shaped system. C, an enlarged reverse view of part of the system shown in B. Sketched from resin burrow casts; Sapelo Island, Georgia.

Upogebia affinis. Identifiable grass fragments have been observed in other burrow casts recovered by us, although mostly in small quantities and without lodgment in any particular chamber or special part of the burrow system.

Comparable detritus has been noted in burrow linings of the thalassinidean shrimp *Neaxius* sp. from Aldabra Atoll, and has been considered a normal aspect of burrow construction (Farrow 1971, p. 468). Unmistakable grass fragments have been found in burrow walls of the stomatopod *Pseudosquilla ciliata* from the Seychelles (Braithwaite & Talbot 1972, p. 281); the significance of these materials is not clear, although they may have been incorporated into the burrow incidentally, from the host substrate.

Perhaps more significant are matted grass blades stored in certain chambers of burrows made by *Callianassa* spp. from Florida and the Bahamas (Shinn 1968, pl. 110, fig. 1), Aldabra Atoll (Farrow 1971, p. 477), and the Seychelles (Braithwaite & Talbot 1972, p. 278). Animals such as the omnivorous polychaete *Nereis diversicolor* and the land crab *Cardiosoma guanhumii* are known to store plant matter for later feeding (Pettibone 1963, p. 177; Herreid 1963); certain marine decapods also consume large quantities of grass (Crichton 1960). But no thalassinidean shrimp are presently known to be true herbivores. Thus, these grass pockets have been interpreted simply as caches of materials too bulky to be removed easily from the burrow (Farrow 1971). This conclusion is reasonable, yet we favor the suggestion by Braithwaite & Talbot (p. 280) that the grass may instead serve as a medium for the culture of edible bacteria. To take this idea one step farther, R. G. Bromley (1974, personal communication) speculated that such bacterial food might be utilized by juvenile offspring rather than, or in addition to, the adults themselves.

Possible fossil analogs

Fossil burrows strikingly similar to those ordinarily constructed by *Upogebia affinis* have been observed abundantly in muddy

Pleistocene sediments of North Carolina (Curran & Frey 1973; Belt, Frey & Welch in press), and probably are common elsewhere in comparable deposits. Ancient structures of this general kind are assigned to the trace fossil genus *Thalassinoides* (see Häntzschel 1975), although numerous organisms other than thalassinidean shrimp are also able to construct such burrows (Bromley & Frey 1974).

Even more striking in the Pleistocene of North Carolina, however, is a type of shrimp-like burrow having a bulbous enlargement from which much smaller burrows radiate (fig. 5). This structure, discovered by Curran (in press), seems to be functionally analogous to that of the postlarval burrows of *Callianassa kraussi* (Forbes 1973) and the excavations presumably made by juvenile *Upogebia affinis* (figs 1 & 2). The ancient structures, in some general respects resembling the larger trace fossil *Phoebichnus trochoides* (Bromley & Asgaard 1972), are closely associated with *Ophiomorpha*; the latter is a fossil analog of the knobby burrows of recent *Callianassa major* (Weimer & Hoyt 1964), *Upogebia pugettensis* (Thompson 1972), and other ethologically similar shrimp. The small structures radiate from thickly lined host burrows that are 2–3 cm in overall diameter; the small burrows, 2–4 mm in overall diameter, have a comparable, proportionately thick lining (fig. 5A, C). These tiny burrows seem to have been constructed by juvenile individuals of the same species of shrimp, presumably having begun their tunneling from within the parent burrow.

Another conceivable analog is the shrimp-like burrow *Ardelia*, from the Permian of Utah (Chamberlain & Baer 1973). The walls of this burrow are perforated in places by profuse blind tubules that radiate from the main tunnels and shafts. The structure has been interpreted, perhaps rightly so, as a primitive equivalent of the knobby walls of *Ophiomorpha* (Chamberlain & Baer 1973). Yet we wonder if the tubules might not represent some equally primitive hatching structure.

Intermediate between *Ardelia* and the Pleistocene burrows is a form of *Ophiomorpha* observed in the Cretaceous of Utah. The morphological and environmental character-

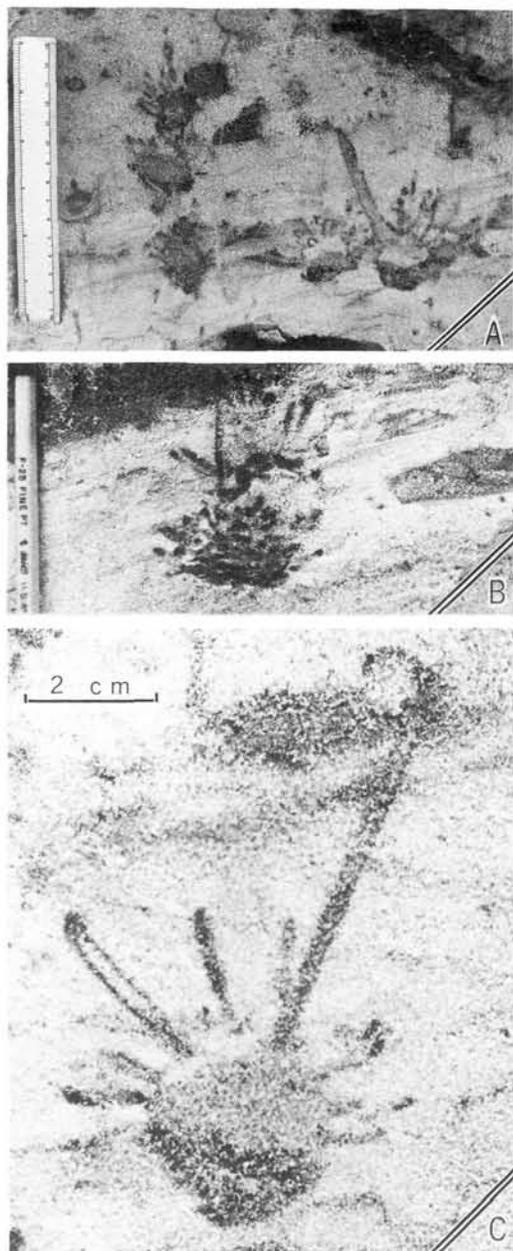


Fig. 5. Clusters of small fossil burrows radiating off supposed parent tunnels. Vertical views. A, B, typical configuration of secondary burrows emanating from horizontal host burrow (ball-point pen ca. 7 mm wide). C, view of characteristic lining of small burrows; in most specimens the host burrow is more thickly lined and has essentially the same composition as the tiny structures. Pleistocene of North Carolina. (Photos courtesy of H. A. Curran).

istics of the overall trace fossil assemblage were reported by Howard (1966, 1972); but no previous mention has been made of horizontal *Ophiomorpha* that, in the Star Point Formation, locally are 'encrusted' by clusters of tiny thalassinoid burrows. The tiny dichotomous burrows resemble the tubules of *Ardelia* in that they occur at many places along the length of the host burrow, rather than being confined to specific bulbous enlargements or other foci; in addition, they seem to be functionally analogous to the Pleistocene structures (fig. 5). The Cretaceous 'tubules' are not conspicuously mammillated and, by themselves, would not be called *Ophiomorpha*. We attribute the wall characteristics mainly to the small size of the burrows and the prospect that they represent only ephemeral, transitory excavations made during the early ontogeny of the tracemaker. But even the large host burrows are less prominently knobbed than typical vertical specimens of *Ophiomorpha* (see Howard 1972, fig. 4).

In general, close associations between seemingly independent burrows of similar proportions but contrasting sizes should also be suspect. An example of this possibility is the juxtaposed very small, intermediate, and normal-size *Thalassinoides* observed by Howard (1966) in the Cretaceous of Utah (fig. 6). Interconnections between the various burrow systems have not been noted, but the successively smaller structures might well represent correspondingly younger generations of the same species of burrower.

Another mode of occurrence of these tiny *Thalassinoides* is indicated in fig. 7. The burrows are clustered in small depressions, which we interpret as primary depositional features originally filled by mud. Initial burrowing evidently was confined to the sand-mud interface. Large *Thalassinoides* are not obviously

Fig. 6. Specimens of the trace fossil *Thalassinoides*, showing distinctly different size classes. Plan views. A, typical large and intermediate-size specimens. B, enlargement of part of A, illustrating unusually small thalassinoid burrows, possibly made by postlarvae or very young juvenile shrimp. (Coin in same position on rock in both photos). Star Point Formation (Upper Cretaceous), Utah (cf. Howard 1966, fig. 14).





associated with these particular specimens, but adjacent rocks yield very similar small burrows adhering to the exterior of large *Thalassinoides*.

Discussion and conclusions

To our knowledge, *Upogebia pugettensis* is the only species of this genus that has been monitored closely with respect to behavior and life functions during early ontogeny (Thompson 1972). In general, its early development is probably typical of many thalassinideans. The eggs hatch as carnivorous planktic larvae that feed actively. Only in the first postlarval stage do the young shrimp settle onto the substrate surface, where they excavate a tiny burrow and assume a life of endobenthic filter feeding.

The burrows of most adult *Upogebia pugettensis* evidently are not interconnected, a trait perhaps less typical of thalassinideans as a whole. Few burrows contain more than one animal, and the individuals pugnaciously defend their territory. Constricted branches have been observed within the burrows; yet these connections are typically shorter and more blunt than those observed within the burrows of *U. affinis*, and their origin and function seem to be different (Thompson 1972).

In the spectrum of thalassinidean adaptations, one extreme is represented by *Callianassa turnerana* of Africa, which annually migrates up freshwater rivers for mating (Monod 1927). Another extreme is the African *C. kraussi*, which has a known salinity range of about 1 to 60 ‰ and which lacks a planktic larva (Forbes 1973, 1974).

Little is presently recorded about the detailed characteristics of the burrow walls made by

these two thalassinideans. If further work should show the exteriors to be knobby, they would be our first undoubted examples of nonmarine and (or) hypersaline associations of *Ophiomorpha*-type burrows (cf. Kennedy & MacDougall 1969). If smooth, they would show the same association for *Thalassinoides*.

The free-swimming larval stage also has been completely suppressed in *Upogebia savignyi* from the Red Sea; the young have an almost adult form when hatched and remain with the adults in the chambers of sponges (Gurney 1937), an unusual habit for shrimp of this family. Several other larval specializations were noted by Gurney (1942). Thalassinideans thus are very plastic genetically, and even more distinctive adaptations of one kind or another are probably widespread among the different species.

For forms such as *Upogebia affinis* that are known to have planktic larvae, the most pressing questions are: (1) can the genotype conceivably be so broad that, under different combinations of environmental stimuli, it can yield two radically different larval phenotypes – one planktic and the other endobenthic, (2) after metamorphosing from planktic or nektobenthic larvae, are the postlarvae stimulated (by metabolites or other factors) to settle in the vicinity of adults, some of the young even entering the burrows of adults and taking up their initial endobenthic existence there, or (3) in the process of pumping water through the burrow system do the adults inadvertently siphon some of the larvae or early postlarvae back into the open burrows, where the young remain during early ontogeny?

Of the three possibilities listed above, the last two offer more plausible explanations for the origin of the small burrows of *Upogebia affinis* observed by us. Although 'accidents' of the kind outlined above must occur, we suspect that settling behavior is a definite factor. The influence of adults upon the settling behavior of postlarvae of numerous kinds of marine organisms is a well known phenomenon (e. g., Johnson 1964, table 1). In this case the interpretation is strengthened by the known gregariousness of *U. affinis*, the documented occurrence of juveniles within adult shrimp burrows (Pearse 1945), and by small satellite

Fig. 7. Tiny thalassinoid burrows localized in circular depressions. Plan views. A, general view of bedding surface, showing typical distribution of depressions. B, enlargement of part of A, showing configuration of the tiny burrows (cf. fig. 6B); the burrows vary considerably in diameter, even at this scale. The raised 'boss' in the center of this depression is an integral part of the overall structure; similar bosses were observed in other depressions containing such burrows. Star Point Formation (Upper Cretaceous), Utah.

burrows that interconnect with larger ones but not with the substrate surface (fig. 4).

Callianassa kraussi and *Upogebia savignyi*, although having remarkably different life styles, are the only thalassinideans presently known to lack a planktic larva. Yet much of the original literature on ecology and behavior of shrimp larvae is vague – valuable works such as those cited by Gurney (1942) notwithstanding – and numerous occurrences are poorly documented. Well-identified specimens taken in plankton tows are unequivocal evidence, of course, but traditional laboratory observations on larval and early postlarval ontogeny are inherently incapable of revealing the kind of behavior in question here. Most of the aquaria used in such experiments contain only water. Little thought is ordinarily given to the prospect that a sedimentary substrate or the burrow of a gravid female might be required in order to evoke a natural response from the animals. We thus suggest that, if the latter experimental design were to be employed routinely, several other shrimps perhaps also would be found either to omit a planktic larval stage and remain inside the parent burrow during early ontogenetic development, or to enter adult burrows upon settlement from the water (cf. Knowlton 1973; Ginsburg & Hardie 1975, fig. 4B; Howard & Frey 1975 b, pl. 14, fig. 46).

The first type of behavior (suppression of a planktic larva) is categorically very different from that of such thalassinideans as *Upogebia pugettensis*, and the adaptation may have necessitated corresponding changes in physiology and trophic specializations. The larvae of *Callianassa kraussi*, unlike planktic ones, do not feed (Forbes 1973). Feeding among active postlarvae has received little study but may be generally similar to that of older shrimp. The behavior of certain species may have evolved even to the point of utilizing plant fragments for the propagation of edible microorganisms (Braithwaite & Talbot 1972). An intriguing possibility is that such behavior is a form of postnatal care or incubation of endobenthic progeny, if not for active larvae or postlarvae then at least for communal juveniles.

Such trophic specializations, whether for juveniles or adults, would be especially useful

among deposit-feeding shrimps in substrates impoverished in organic detritus. Examples of this situation were discussed for the *Rhizocorallium*-animal by Sellwood (1970, p. 494–495) and for the present-day lugworm *Arenicola* by Jacobsen (1967), except that here the paucity of edible detritus was compensated by filter-feeding behavior.

In any case, the utilization of bacterial food by shrimp would be difficult to prove experimentally. Some of the questions that we might ask include: (1) which of the bacteria growing on this organic matter are actually edible by shrimp, (2) what is the nutritive value of these bacteria, and (3) by what mechanism does the organic matter accumulate in the shrimp burrows (is the behavior of the shrimp passive or active in this regard)?

In the fossil record, as among resin casts such as ours, one of the major problems in documenting a suspected occurrence of juvenile shrimp burrows is to discern whether the tiny burrows were made by the same species as the large burrow, or by a small commensal or subsequent inhabitant of the burrow. In addition to similarities in overall burrow geometry and configuration, the characteristics of wall linings would be important.

One advantage in working with fossil examples is that interconnected burrows, whether permanently maintained or later atrophied by growing juveniles, ordinarily would remain discernible. Because diagenesis generally enhances trace fossils, even cut-offs and other abandoned parts of burrows are typically well preserved (e. g. Frey 1975, figs 2.2, 2.9), and the sequence could be determined by cross-cutting relationships. Other criteria would have to be evaluated independently, on the merits of given specimens. (See Bromley & Frey 1974.)

Relationships among the various types of *Thalassinoides* illustrated in figs 6 & 7 remain ambiguous, as does the significance of other *Thalassinoides* systems containing components that vary widely in diameter (e. g., Kennedy 1967, p. 142). These examples could well represent gradually merging systems made by different generations of the same species of burrower. But that in itself does not indicate whether the systems originated independently,

by juveniles that settled from the water column onto the substrate surface, or whether the smaller systems originated endobenthically, from the tunnels of parent burrowers. In later stages of development the latter would be difficult to differentiate from originally independent burrows that eventually intersected one another. The nature of the connective branches, especially their relation to the substrate surface, and the presence and morphology of apertural necks, may prove to be valuable clues in this respect.

A potentially misleading association between burrows is exemplified by the trace fossil *Chondrites*, which is commonly found in close proximity to, or in the wall lining of, shrimp-like burrows (e. g., Kennedy 1967, pls. 5, 6; Bromley & Frey 1974, fig. 5). These *Chondrites* could easily be mistaken for post-larval shrimp burrows.

Many of the characteristics of individual burrows are also a reflection of local sedimentary conditions (e. g., Farrow 1971, figs 12–15). These too would have to be recognized and evaluated in any study of the ontogenetic development of burrow systems.

As a final note of caution, fossil examples of "grass-storage" chambers might be difficult to distinguish from sod clasts such as those observed by Howard & Frey (1973, fig. 3b; 1975 b, fig. 6. E) in Georgia estuarine sediments. Some of these rounded clasts consist of nearly pure peaty material; we can easily envision a shrimp burrow merely intersecting the edge of such a ball, producing the spurious effect of an irregular chamber excavated and stocked by the shrimp. Whether the shrimps would actually utilize this deposit for bacterial cultures remains unknown.

Further work, on both recent and ancient examples, will hopefully yield better criteria for resolving the numerous ambiguities outlined above. At any rate, the work that has been done clearly illustrates the potential preservability and considerable importance of postlarval shrimp burrows in paleoecologic reconstructions, and helps explain trace fossils that otherwise would be difficult to interpret. It also opens up a comparatively new field for ontogenetic, ecologic, and ichnologic investigation.

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Dansk sammendrag

En gravegang af *Upogebia affinis* fra Sapelo Island, Georgia, U.S.A. er forsynet med kammerformede udvidelser. Fra kamrene udgår talrige små tunneller som grener sig på karakteristisk thalassinoid vis. Disse tunneller tolkes dannet af unge individer af *Upogebia affinis*.

Eksempler på det samme fænomen er rapporteret for *Callianassa kraussi* fra Syd Afrika, og mulige fossile analoger er observeret i Nord Carolinas pleistocæn og i Utahs perm og kridt.

I nogle *Upogebia affinis* gangsystemer varierer visse elementer betydeligt i diameter. Disse gange, der forbinder sig med hovedsystemet gennem indsnævrede åbninger, repræsenterer en vækstserie fra gange gravet af juvenile dyr til de normale gange gravet af (adulte) fuldvoksne individer.

Som en hypotese foreslås at visse krebsdyr muligvis udnytter planterester i gravegangen til kultur af spiselige mikroorganismer.

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