

THALASSINID SHRIMP BURROWS : ECOLOGICAL SIGNIFICANCE OF SPECIES-SPECIFIC ARCHITECTURE

LES TERRIERS DES CREVETTES THALASSINIDES : SIGNIFICATION ECOLOGIQUE DE L'ARCHITECTURE SPECIFIQUE DES ESPECES

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ABSTRACT

Burrow architectures of temperate and tropical burrowing shrimp of the tribe Thalassinidea were investigated by use of resin casting techniques and assessed from published literature in order to evaluate trophic status and feeding mode in relation to burrow morphology.

All thalassinids studied demonstrate species-specific burrow architecture. Three major ecological types have been identified: filter/suspension feeders, deposit/detritus feeders and seagrass/algae harvesters. Filter/suspension feeders, found in temperate habitats, typically build shallow, simple U-shaped or Y-shaped burrows and obtain their nutrition from plankton or suspended particulates. Detritus/deposit feeders, most often found in the tropics, usually construct temporary, deep, architecturally complex burrow systems and continuously process vast amounts of sediment to extract organic material. Fine-grained (\leq ca 1.0mm) processed material is pumped to the sediment/water interface where it accumulates as volcano-shaped mounds. These mounds are often the most conspicuous features of shallow tropical or subtropical lagoons. The third ecological type, the seagrass/algae harvesters, are inconspicuous members of their environment in that they build no mounds. Instead their burrow openings are typified by a simple hole(s), often temporary and unpredicable in location. In tropical habitats species of this group are found both in seagrass beds and at the edges of patch reefs. They capture detrital plant material drifting past their burrow openings, storing it in deep burrow chambers, possibly for the subsequent harvesting of bacteria or fungi. Their burrows are usually long, straight and deep with few accessory chambers.

The significance of these three extant ecological types is discussed in relation to the paleontological interpretation of lebensspuren from world-wide temperate and tropical shallow water habitats.

RESUME

L'architecture des terriers de crevettes fouisseuses Thalassinides (Crustacea, Decapoda) a été étudiée en zones tempérées et tropicale, par des moulages à la résine, et l'analyse de la littérature, parue à ce sujet, pour évaluer la relation entre le mode de nutrition et la morphologie du terrier. Tous les Thalassinides étudiés construisent des terriers dont la structure est caractéristique de l'espèce. Trois principaux types écologiques ont été identifiés: les filtreurs/suspensivores, les détritivores et les récolteurs de végétaux marins (algues, phanérogames).

Les filtreurs/suspensivores, situés principalement en zone tempérée, construisent des terriers peu profonds, typiquement en forme de U simple ou de Y et se nourrissent de plancton et de particules en suspension.

Les détritivores, pour la plupart situés en zone tropicale, construisent des terriers temporaires, profonds et d'une structure complexe. Ils remuent de grandes quantités de sable pour en extraire les particules organiques dont ils se nourrissent. La fraction fine ($<$ ca. 1.0mm) est expulsée à la surface du sable où elle s'accumule en formant des tumuli ressemblant à de petits volcans. Ces tumuli sont souvent le trait dominant des zones sédimentaires dans les lagons peu profonds.

Le troisième type écologique, les récolteurs de macro-débris végétaux, est plus discret car les espèces de ce groupe ne font pas de tumuli. L'entrée de leur terrier est un simple trou (parfois plusieurs), souvent temporaire et dont le lieu d'apparition est difficile à prévoir. En zone tropicale, ce groupe est situé dans les herbiers de phanérogames et/ou à proximité des patates coralliennes isolées. Les macro-débris végétaux qui passent à proximité de l'entrée du terrier sont récoltés et stockés dans des chambres profondes, probablement en vue d'une récupération ultérieure des bactéries et/ou des champignons. Les terriers sont généralement longs, droits et profonds, avec peu de chambres latérales.

La discussion porte sur la signification de ces trois types écologiques en relation avec l'interprétation paléontologique des traces fossiles d'activité animale (lebensspuren), caractéristiques des anciens niveaux littoraux, tant en zone tempérée que tropicale.

INTRODUCTION

Thalassinid shrimp are some of the most ubiquitous and, surprisingly, some of the most ignored animals in nearshore marine environments. They are found abundantly in the soft sediments of nearly every temperate and tropical low energy habitat that has been studied. Furthermore, they are not only abundant, but because many of these species transport vast amounts of sediment to the surface in the form of volcano-shaped mounds, their presence is usually extremely conspicuous. Previously, most interest in these species has been directed at their paleontological significance as indicator organisms of ancient littoral or shallow neritic environments (e.g. - Weimer & Hoyt, 1964; Frey, 1970; DeWindt, 1974; Frey *et al.*, 1978). And, with the exception of a few early natural history studies (Stevens, 1928, 1929; McGinitie, 1934) and some recent works on the impact of their bioturbational activities on community ecology (Brenchley, 1981, 1982; Bird, 1982; Suchanek, 1983), their modern ecological significance has been largely overlooked. Two major reasons account for this neglect. First, they are extremely secretive, living in permanent or semi-permanent burrows usually several centimeters to several meters below the sediment/water interface. Second, they move quickly and, because of the unstable nature of the soft sediments they occupy, are extremely difficult to collect and to study.

It is becoming increasingly evident that these species not only extensively modify their physical environment, but also have intimate ties to carbon, nitrogen and sediment budgets in nearshore environments (Suchanek, 1983; Suchanek *et al.*, 1985b). Therefore, it is important that we understand, as accurately as possible, the ecological and energetic relationships of these abundant, actively burrowing crustaceans.

Here I review published data and present new data regarding the species-specific morphology of thalassinid shrimp burrows from both temperate and tropical habitats around the world. In addition I present information on the ecological significance of three major burrow and feeding types.

BURROW MORPHOLOGIES

Techniques for studying burrows:

Early researchers used flexible willow branches to trace the path of burrows beneath the sediment surface, while positive molds of burrows were obtained using cement or plaster of paris (Stevens, 1928, 1929). With the advent of more durable polyester catalyst resins, a new era in burrow molding techniques began (Shinn, 1968), allowing a more accurate accounting of shape, size, depth, lateral extent, and fine-scale features of burrow morphologies.

High-density polyester resins can be used in both intertidal (Thompson, 1972) and subtidal environments (Suchanek, 1983; Suchanek *et al.*, 1985b). With this technique, resin is poured into burrows from the sediment surface and allowed to harden at least 24 hrs. The positive burrow casts are then removed by careful digging in intertidal areas or by using a suction dredge subtidally. Most polyester bonding or molding resins will suffice; the critical factor is that they must be more dense than seawater in order to flow downwards into the deepest reaches of the burrow system.

Another technique, the "archaeological" method, involves direct observation of burrow features while carefully excavating sediments, layer by layer (de Vaugelas, 1985). Lateral sediment movement is prevented by inserting sheet metal vertically into the sediment at the edges. One advantage here is that passages blocked with sediment or detritus can be more easily observed than by resin casting. Disadvantages are limited depth accessibility because of shifting sediments, and loss of detail regarding the burrow walls.

Burrow classifications:

A review of the literature on burrow morphologies for the most common tropical and temperate thalassinid shrimp is provided in Table 1. Based on features visible on the sediment surface, these shrimp burrow systems can be classified into two major groups: those with and those without significant mounds. Many species produce volcano-shaped mounds of discarded sediment at their excurrent opening. This sediment is often a combination of a) sediment being removed during the construction of tunnels or chambers, and/or b) sediment (either recently obtained from the surface via incurrent depressions or from depth) that is being sorted to extract organic detritus for food. Mounds can range in size from small dimples on the surface to large cones of sediment over 30cm high. With further information on the trophic relationships of the resident shrimp, burrow systems without mounds can be further divided into two subgroups: those designed for filter feeding and those used to store harvested seagrasses and/or algae.

All thalassinid shrimp for which *both* their feeding mode and burrow morphology are known can fit within a scheme of three basic ecological types, described below.

Filter/Suspension Feeders: (Temperate Habitats almost exclusively)

This group is characterized by having relatively simple, permanent burrows that are typically U-shaped or Y-shaped (Fig. 1A). This is not surprising since most infaunal filter feeders have evolved such a burrow or tube morphology for efficient, unidirectional water flow. Because these species do not process much or any sediment, they also do not develop any significant excurrent mound features. The largest mounds found associated with burrows of these species are only 3-8cm high and are likely the result of either initial tunnelling or burrow "house-keeping" activities (i.e. - removing sediments or debris that have inadvertently fallen into the burrow). Species known to fit into this category are mostly from the temperate zone: *Callianassa affinis* (found in high-energy boulder fields in California), *Callinectes jousseaumei* (from the Gulf of Aqaba, Red Sea), *Upogebia pugettensis* (west coast United States), and possibly *Callianassa maior* (southeast United States) and *Upogebia pusilla* (Adriatic Sea). The burrow morphology of *Callinectes jousseaumei* (described by de Vaugelas, 1985) is more complex than expected and represents the only exception for burrows associated with this mode of feeding. This species may use both suspension and detritus feeding modes (J. de Vaugelas, pers. comm.). *Callianassa maior* also has a simple burrow morphology, but its feeding mode has not been

TABLE 1. Geographic distributions, habitats and statistics on burrow systems for well known thalassinid shrimp. A dash (-) indicates that no data was found. A question mark (?) indicates incomplete, ambiguous or questionable data. Under the category water depth, "I" indicates intertidal distribution. Numbers listed under "sources" refer to numbered references at the end of this paper. An asterisk (*) under "sources" indicates Suchanek (unpublished data).

TROPICAL OR SUBTROPICAL:		water	burrow		#	mound	grass or	grass	are		
species	location	depth	depth	width	diam	surface	height	sediment	in	burrows	sources
		(m)	(cm)	(cm)	(mm)	openings	(cm)	in chambers	lining	complex	
<u>Callinassa</u>											
<i>C. sp.</i>	Florida & Bahamas	I-10	100	60	20-30	2	30	both	no	yes	8,29
<i>C. sp.</i>	Marshall Islands	3-60	80	>100	32	≥2	20	-	no	yes	33,35,*
<i>C. sp. 1</i>	Seychelles	I-?	30	9	6-8	2	1-2	-	-	yes	2,8
<i>C. sp. 2</i>	Seychelles	I	38	30	15-20	-	10-15	both	-	yes	2,8
<i>C. acanthochirus</i>	Virgin Is.	I-10	-	-	10-20	≥2	none	-	-	-	26,32,*
<i>C. quassetinga</i>	Brazil	-	>60	30	28	2	none	-	-	no	8,28
<i>C. longiventris</i>	Virgin Is.	3-10	150	≥200	30	≥2	none	grass	no	no	32,*
<i>C. quadracuta</i>	Virgin Is.	1-10	-	-	-	2	small	-	-	-	32,*
<i>C. rathbunae</i>	Virgin Is.	1-10	>1.5	50	30	2	27	sediment	no	yes	27,32,*
<u>Callichirus</u>											
<i>C. jousseumei</i>	Red Sea	I-10	90	50-100	30	3	5	no	no	yes	38
<i>C. laurae</i>	Red Sea	I-50	150	300	30	2	40	both	no	yes	38,39
<u>Neaxius</u>											
<i>Neaxius sp.</i>	Seychelles	-	50	40	1-10	1-2	none	grass	yes	no	8,9
<u>TEMPERATE:</u>											
<u>Axius</u>											
<i>A. serratus</i>	Nova Scotia	7-77	>250	50	10-30	1	none	no	yes	no	8,23
<u>Callinassa</u>											
<i>C. affinis</i>	California	I	-	-	-	-	none	no	no	no	8,20
<i>C. biformis</i>	Georgia	I-25	-	-	4-10	-	-	-	-	yes	8,13,16,17,26
<i>C. californiensis</i>	U.S. (west coast)	I	≥50	-	-	2-4	3-8	no	no	no	1,4,19,20,25,30,*
<i>C. filholi</i>	New Zealand & Australia	I-3	>45	-	-	>2	small	-	-	-	6
<i>C. gigas</i> (= <i>C. longimana</i>)	Puget Sound, Washington	I	-	-	-	2?	none	-	-	-	20,30,*
<i>C. kraussi</i>	S. Africa	I	-	-	-	1?	none	-	-	no	8,10
<i>C. major</i>	United States (southeast)	I-5	215	180	22	1-10?	0.4	no	no	no	8,11,24,41
<i>C. stebbingi</i>	Adriatic	sub-	>25	-	9	3-4	?	no	no	-	21
<u>Upogebia</u>											
<i>U. affinis</i>	Georgia & N. Carolina	I-15	50	200	15	1-8?	none	no	yes	no	8,14,17,22,26
<i>U. pugettensis</i>	U.S. (west coast)	I	90	72	33	≥2	none or small	no	no	no	1,4,8,18,20,30,36
<i>U. pusilla</i> (= <i>U. litoralis</i>)	Adriatic Sea	I-45	48	22	22	2-4	none	yes	no	no	8,21

studied adequately. The predominance of these species in the temperate zone only is very likely a consequence of the high level of primary and secondary productivity of temperate waters compared to that of the tropics.

Deposit/Detritus Feeders:
(Tropical Habitats almost exclusively)

Species in this group typically process large volumes of sediment in order to extract significant amounts of organic detritus (Bird, 1982; Suchanek 1983; de Vaugelas & de Saint-Laurent, 1984; Suchanek *et al.*, 1985b). They are found most often in tropical habitats and their large volcano-shaped mounds of discarded sediment, piled at the excurrent opening of the burrow system, are usually the most conspicuous physical features of their environment. It is therefore surprising that so few ecological studies have been done on these species. Sediment processing occurs 24 hrs/day and can reach 3.4 kg/m²/day (Roberts *et al.*, 1982; Suchanek, 1983). The architecture of these burrow systems is, again, quite species-specific (see Dworschak, 1983 for drawings of many such species) the burrows typically having very complex morphologies (Fig. 1b). This complexity may be a consequence of the sediment sorting process itself. For *Callianassa rathbunae*, smaller particles (grain size < ca. 1.0mm) are gleaned for organic matter and then discarded by pumping them to the surface using pleopod currents (Suchanek, 1983). Larger particles (shell or coral fragments) that are either too heavy to be moved by the pleopods or are too large to fit through the small excurrent aperture, are stored in deeper refuse chambers.

In addition, because tropical carbonate sediments are so nutrient-poor, it is suspected that these species may regularly alternate the locations of their incurrent openings in order to utilize sediment from a broader area (Suchanek *et al.*, 1985b). Therefore, the active portions of these burrow systems tend to be rather temporary in nature, both with respect to the incurrent and excurrent openings, as well as the deeper storage chambers. Species that fit within this category are: *Callianassa* sp. (from Enewetak Atoll, Micronesia - Suchanek *et al.*, 1985b), *C. californiensis* (west coast United States), *C. filholi* (New Zealand and Australia), *C. quadracuta* (Virgin Islands, Caribbean Sea), *C. rathbunae* (Virgin Islands, Caribbean Sea), *C. stebbingi* (Adriatic Sea) and *Callinectes lauræ* (Gulf of Aqaba, Red Sea).

Seagrass/Algae Harvesters:
(Temperate and Tropical Habitats)

Little is known of the trophic and ecological significance of species in this group. They can be found in both temperate and tropical habitats, but tend to be inconspicuous members of the community because they do not produce significant mound structures. Their burrows tend to be rather permanent, but some of their openings to the surface may be blocked off for unpredictable periods of time (Suchanek, in prep). These species harvest seagrasses and/or algae, chop the blades into small pieces (several mm to several cm long) and either incorporate them into the burrow wall or store them in deep chambers. Their burrow systems are characteristically simple, long, relatively straight and often deep (Fig. 1c). Whether they harvest the seagrasses

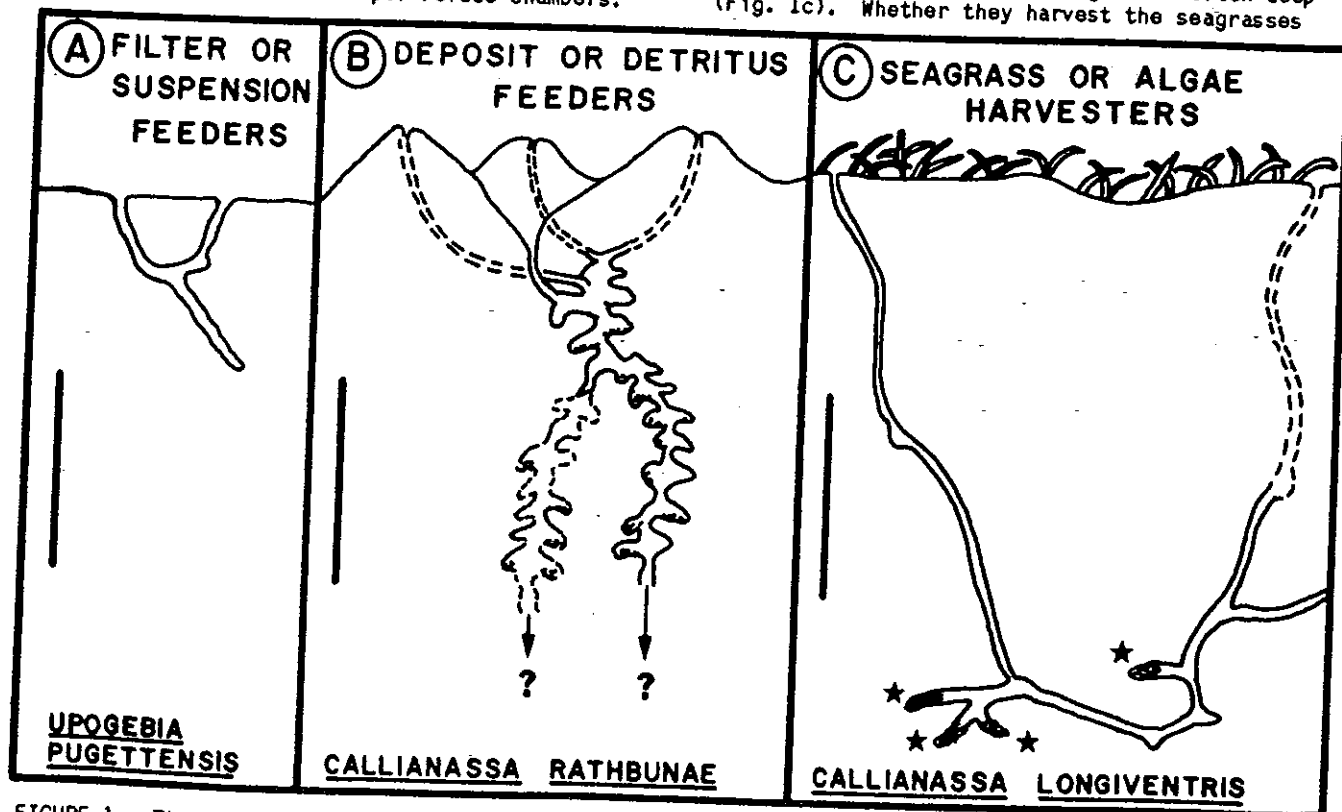


FIGURE 1. Three ecological types of thalassinid shrimp burrows. (A) from Thompson (1972), (B) from Suchanek (1983), (C) from Suchanek (in prep). In each diagram the vertical bars represent 50cm. Dashed lines indicate suspected burrow positions not filled by resin. Stars in C represent chambers where seagrasses and algae are stored.

and algae to consume directly (Pearse, 1945), for the nourishment of juveniles (R.G. Bromley in Frey & Howard, 1975), or as a medium on which to culture fungi and/or bacteria (Braithwaite & Talbot, 1972; Frey & Howard, 1975; Ott et al., 1976) is still in question.

One fact is clear: contrary to previous reports (Farrow, 1971; Frey & Howard, 1975) the caches of macerated seagrass and algae do not simply represent materials that have inadvertently fallen into the burrow and are too bulky to be easily removed. Suchanek (in prep) has successfully "hand-fed" blades of the seagrasses *Thalassia testudinum* and *Syringodium filiforme* and the algae *Dictyota* spp. to *Callianassa longiventris* in the Caribbean. This species waits at the mouth of its burrow for drifting plant debris, vigorously snatches such blades as available, disappears to store them in deep chambers 1-2m below the sediment surface (see stars in Fig. 1c), and returns within 15-20 sec to collect more. The following species have similarly long/straight burrow morphologies and/or store seagrasses or algae in their burrows: *Axius serratus* (Nova Scotia), *Callianassa* sp. (Florida and the Bahamas - Shinn, 1968), *Callianassa acanthochirus* (Virgin Islands, Caribbean Sea), *Upogebia affinis* (Georgia and North Carolina), *U. pusilla* (Adriatic Sea), *Callinectes laurae* (Red Sea), *C. armatus* (French Polynesia - de Vaugelas et al., 1985) and probably *Neaxius* sp. (Aldabra, Seychelles - Farrow, 1971).

For *Upogebia affinis*, stomach analysis yielded 30% algae (*Ulva*) and 0.5% bacteria in addition to a substantial amount (59%) of organic debris (Pearse, 1945). For *Axius serratus*, no published data were found on its feeding mode, although it incorporates eelgrass into the burrow lining (Pemberton et al., 1976). Similarly, little information exists on the burrow structure for *Callianassa acanthochirus*, but M.H. Bundy and Suchanek (unpublished data) have "hand-fed" seagrasses to this species in the same manner as described for *C. longiventris* above. It is suspected, therefore, that all species that collect and incorporate plant debris into their burrow system do it intentionally and likely for the purpose of feeding, either directly or for culturing fungi or bacteria. This would be a fruitful area for future research.

DISCUSSION

From the aforementioned data it appears that filter/suspension feeding thalassinids occur mostly in temperate habitats and, although they make burrows with species-specific architecture, they all have rather shallow, simplistic U-shaped or Y-shaped burrows. Also uniquely characteristic are the deposit/detritus feeders in mostly tropical habitats who have exceptionally complex and deep burrows. The third ecological type, the seagrass/algae harvesters, from both temperate and tropical environments, can be recognized by the significant accumulation of plant debris in tunnel walls or deep chambers. Furthermore, in addition to the three general ecological/burrow types, it appears that nearly all of the extant species have their own species-specific architecture (see Dworschak, 1983 for a comparison of many species).

The three ecological types can have very different effects on their biological and physical surroundings. All types, simply by the nature of their occupying physical burrow space in the sediment, may impact the biological community in these soft sediments (Branchley, 1981, 1982). Filter/suspension feeders consume living and detrital suspended matter, but they appear to alter significantly neither the organic content of the sediment nor the infaunal community structure (Bird, 1982). These species seem to have little effect on the sediment depositional regime. Deposit/detritus feeders, on the other hand, can not only lower the level of entrained organic material in the sediment available to other species (Bird, 1982; Suchanek, et al., 1985), but can also process so much sediment that they control sediment grain size, transport, mixing, and deposition (Roberts et al., 1982; Suchanek, 1983; Tudhope & Scoffin, 1984) in addition to negatively impacting other populations of animals (Stevens, 1929) or plants (Suchanek, 1983). Coarse sediment debris stored in these deep chambers can also result in regularly spaced bedding planes of coarse and fine sediment (Suchanek, 1983). Finally, the burrows of seagrass/algae harvesters (which collect drifting detrital plant material), can represent a significant nutrient "sink" in shallow nearshore environments potentially "robbing" these carbon and nitrogen sources from other shallow water or deep-sea species (Suchanek et al., 1985a; Suchanek, in prep).

With regard to their paleontological significance, thalassinid shrimp produce conspicuous and geologically important biogenic structures (lebensspuren) in the form of burrows that are characteristic of specific depositional environments (Bromley & Frey, 1974; DeWindt, 1974; Howard & Frey, 1975; Frey et al., 1978). With the abundance of thalassinid shrimp in both temperate and tropical habitats alike, the ecological categories outlined here for modern thalassinids should have world-wide application for aiding in the interpretation of ancient lebensspuren. When the general and/or specific burrow types described above are found in fossil form, the ecological data presented here should permit a more accurate interpretation of the nature of the ancient local environment and the biological community that existed at that site.

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