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The Role of Tegumental Glands in Burrow Construction by Two Mediterranean Callianassid Shrimp

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With 4 Text-Figures and 2 Tables

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Abstract

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Two species of Mediterranean callianassid shrimp (*Callianassa candida* and *Callianassa tyrrhena*) have been observed in aquaria to work sediment into the burrow wall while manipulating it with the mxp3, P2, and P3. Histological sections of the appendages involved in manipulating the burrow wall show numerous multicellular glands ("rosette glands"). SEM investigations of the appendages reveal surface pores with emanating mucus threads. These observations suggest that mucus excreted from tegumental glands in mxp3, P2, and P3 is used to stabilise the burrow wall.

Introduction

Tegumental glands are a ubiquitous feature of the crustacean cuticle (see summaries in STEVENSON 1985; FELGENHAUER 1992). These glands may be unicellular, tricellular, or multicellular. The latter type often described as "rosette glands" is very common in decapods and has been studied in detail (e.g. JOHNSON & TALBOT 1987; ALEXANDER 1989; MCKENZIE & ALEXANDER 1989; FELGENHAUER 1992; FELDER & FELGENHAUER 1993). Several functions have been attributed to the tegumental glands: secretion of epicuticle, tanning of the integument, mucus production for feeding lubrication or food entanglement, cement production for egg attachment, or production of a bacteriostatic and antifouling agent (ALEXANDER 1989; FELGENHAUER 1992; FINGERMAN 1992). Although earlier papers suggest the function of tegumental glands (as "Kittdrüsen") in stabilising the burrow wall (BRAUN 1878; BOHN 1889; LUTZE 1938), this function has been ignored in all recent reviews.

This study deals with observations on the burrowing behaviour of two species of callianassid shrimp, the occurrence of tegumental glands and their pores on the appendages involved in wall construction using histological and SEM techniques, and SEM investigations of the burrow wall.

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Material and Methods

Callianassa tyrrhena (PETAGNA 1792) occurs in the Eastern Atlantic from the North Sea and the Kattegat to Mauritania, and is common in the entire Mediterranean (HOLTHUIS 1991). *Callianassa candida* (OLIVI 1792), a species also known as *C. pontica* CZERNIAVSKY 1884 or *C. pestae* DE MAN 1928, has been reported from the Mediterranean and the Black Sea.

Specimens of both callianassids were sampled with a yabby pump (MANNING 1975) at Lido di Staranzano, a tidal flat near Monfalcone, Italy (for details on habitat see DWORSCHAK 1987a). Here, *C. candida* occurs in the upper intertidal, whereas *C. tyrrhena* can be found in the lower intertidal and shallow subtidal.

For light histology, appendages were fixed in marine Bouin's fluid for at least 48h and dehydrated in graded ethanol solutions. Paraffin sections (5–7 μm) were stained with haematoxylin/eosin, Alcian blue, or Heidenhain's azan. Microphotographs of sections were taken with a Polyvar (Reichert-Jung).

Specimens for SEM were preserved in 4% formaldehyde-seawater or glutaraldehyde, dehydrated in graded ethanol solutions, critical point dried, coated with gold, and viewed in a JEOL JSM-35 at 25 kV.

Samples of burrow wall sediment for SEM were taken by pressing stubs with silicone cement gently against the burrow wall *in situ*, fixed with a 4% formaldehyde-seawater solution, rinsed with water, dehydrated in graded ethanol series, air dried, coated with gold, and viewed in a JEOL SM-35 at 15 kV (GRANT & BATHMANN & MILLS 1986).

Results

Burrowing Behaviour

In limnoria filled with natural sediment, *Callianassa candida* and *Callianassa tyrrhena* immediately begin constructing a new burrow. During the initial phase, the animals are often surrounded by a cloud of mucus. A simple burrow is completed between 6 and 24 h. In an established burrow, the animals are nearly continuously engaged in transporting sediment from one part of the burrow to another (DWORSCHAK 1987b).

Sediment is carried in the basket formed by the 2nd pereiopods and is handled between the operculiform mxp3 which are held in the shape of a V. The last three slender articles of the mxp3 (dactylus, propodus, and carpus) push the sediment ventrally onto the burrow wall. The pincers of P2 move forward and sideward along the outer face of the mxp3 and put the sediment in place while the broadened propodi of P3 smoothen the sediment which has been worked into the burrow wall. Ventrally bent antennulae prevent sediment from pouring out of the basket while the shrimp work on burrow roofs. Due to this plastering activity, the burrow wall in aquaria often shows a distinctly different colour than the surrounding sediment, especially on roofs of mainly horizontal burrow parts (Fig.1).

Fig. 1. *Callianassa tyrrhena* in a burrow constructed in a limnorium. – Note fine material on roof (arrow). Scale is 1 cm.

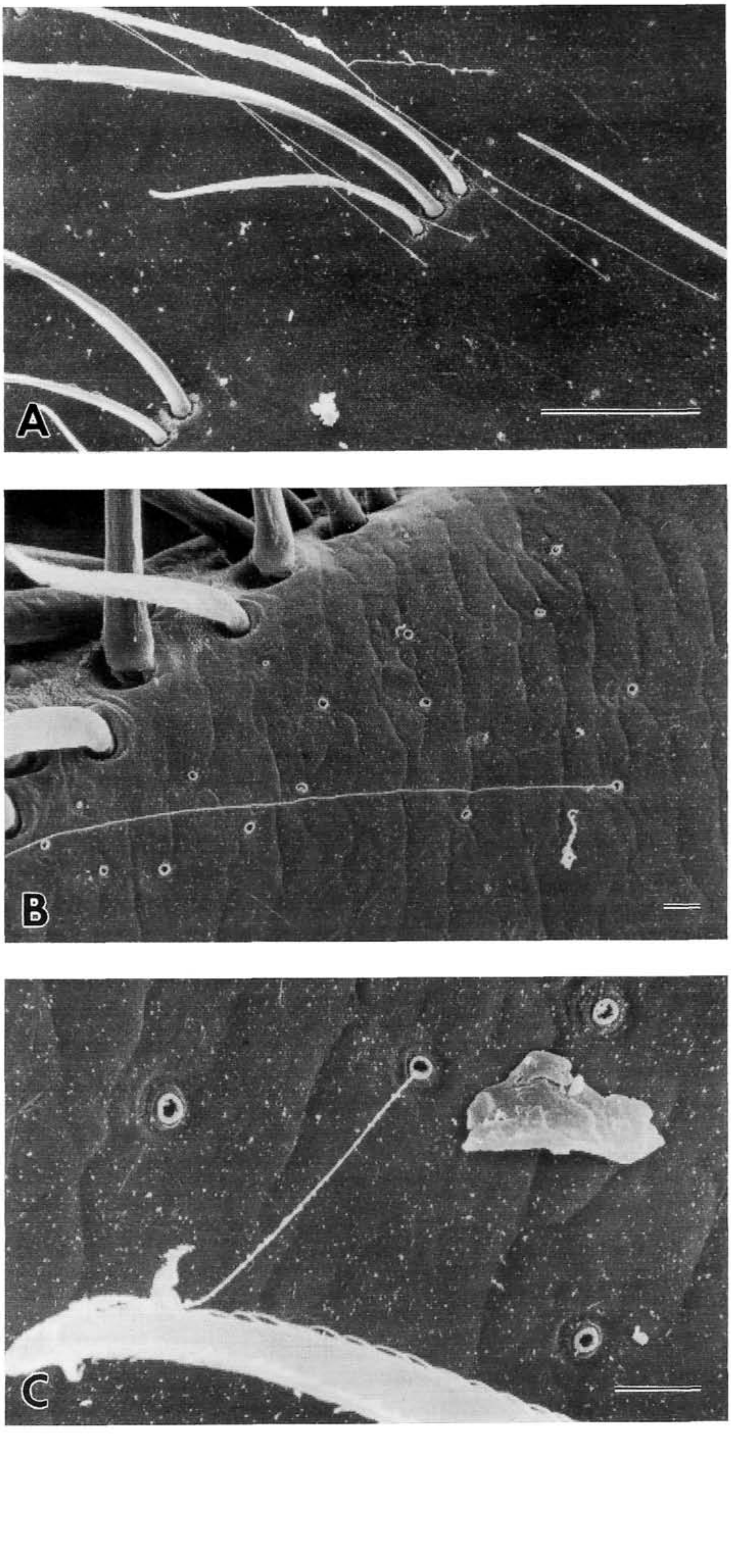

Fig. 2. *Callianassa tyrrhena*, SEM-photographs. — A. Inner surface of the propodus of P3; note pores and mucus threads leading to setae at lower edge (upper left corner); scale is 100 μm. — B. Inner surface of the dactylus of P2; note mucus thread leading to setae on upper edge; scale is 10 μm. — C. Inner surface of the dactylus of P2; scale is 10 μm.

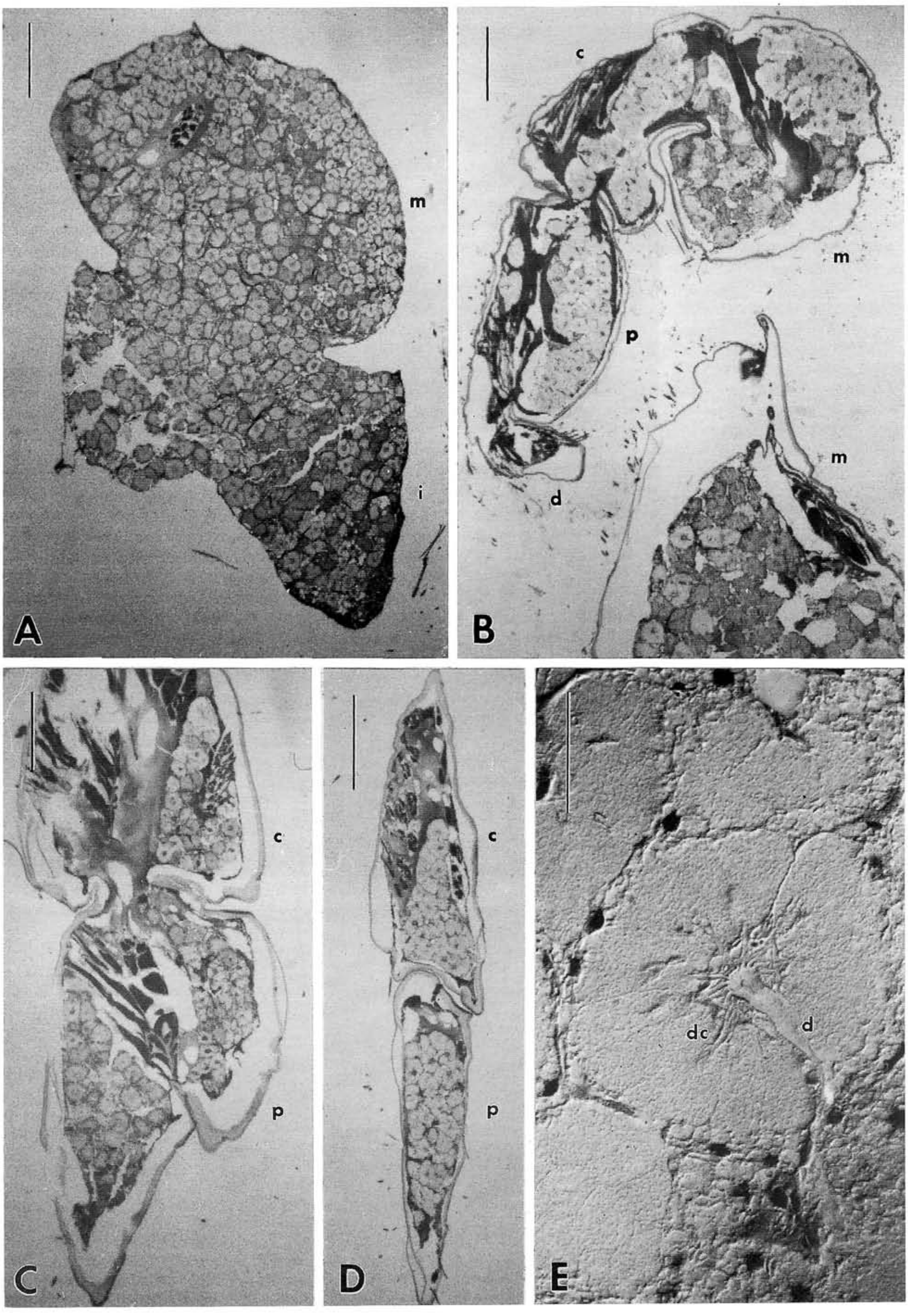

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Table 1. Distribution of pores/mucus threads at the surface of several appendages of *Callianassa tyrrhena*. — Symbols: + present; - not detected; blank, not investigated

article	dactylus	propodus	carpus	merus	ischium
append-age					
P 2	+	+	+	+	
P 3	+	+	+		
P 5	–	–	–		
mxp 3				–	+

Table 2. Distribution of glands in histological sections of several appendages of *Callianassa tyrrhena* and *Callianassa candida*. — Symbols: +++ between 50 and 90% of sectioned area; ++ up to 50% of area; + smaller groups of glands; blanks, not investigated.

article	dactylus	propodus	carpus	merus	ischium
append-age					
P 2	+	++	++	-	
P 3	+	++	++	-	
mxp 3	+	++	++	+++	+++

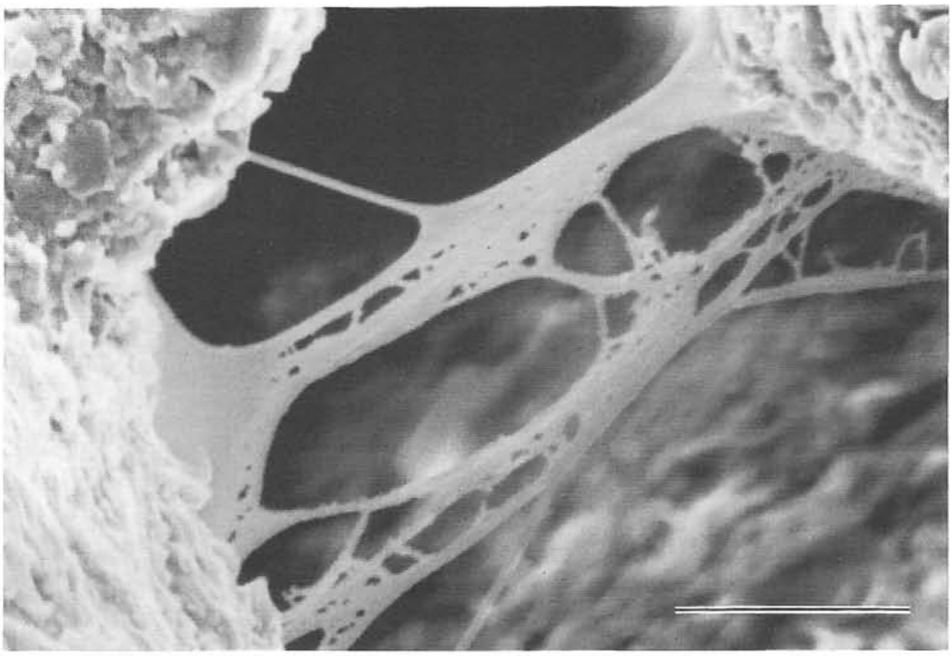

Fig. 4. SEM-photograph of burrow wall sediment. — Note mucus between sediment grains. Scale is 10 µm.

SEM of Appendages

SEM-photographs show the occurrence of pores at the surface of nearly all the appendages investigated (Tab.1).

◀

Fig. 3. A. *Callianassa candida*, left mxp3, longitudinal (sagittal) section through central region of ischium (i) and merus (m). — B. *Callianassa tyrrhena*, left mxp3, longitudinal (sagittal) section through upper region showing merus (m), carpus (c), propodus (p), and dactylus (d). — C. *Callianassa candida*, left P2, oblique longitudinal (sagittal) section through distal part showing carpus (c) and propodus (p). — D. *Callianassa candida*, P3, transverse section through carpus (c) and propodus (p). — E. *Callianassa candida*, P3, cross section through central region of carpus showing one "rosette gland" in detail. Note drainage canals (dc) and main duct (d). — Scale is 500 µm in A–D, 30 µm in E.

These pores are obvious on the inner and outer sides of dactylus, propodus, merus, and carpus of P2 as well as on the inner side of dactylus, propodus, and carpus of P3 (Fig. 2A–B). The diameter of the pores is approximately 2 µm. In many cases a mucus thread with a braided appearance (0.5–0.75 µm thick) leading to the setae is visible (Fig. 2B–C).

Histological Sections

The histological sections reveal glands in all articles of all appendages investigated. Gland diameter is quite uniform and ranges between 100 and 130 µm. In the case of the mxp3, nearly the entire appendage consisted of glandular tissue (about 70 "rosette glands" across a longitudinal section of two articles an estimated 250 to 300 glands when extrapolating for the whole volume of these two articles) (Fig. 3A–B). Glandular structures are also very dense in the propodi of the P2 and P3 (Fig. 3C–D), whereas other articles bear only smaller groups of glands (e.g. only one "rosette gland" in the dactylus of mxp3). The distribution of glands in the appendages is summarised in Tab.2. The glands show the typical structure of "rosette glands", with single cells grouped around a central duct (Fig. 3E).

SEM of the Burrow Wall

Sediment grains of the burrow wall of *C. tyrrhena* are often connected by mucus threads (Fig. 4). Such particle-binding secretions have not been observed in ambient sediment.

Discussion

"Rosette glands" in the appendages of *Callianassa candida* and *Callianassa tyrrhena* are quite similar in structure to the glands described previously in other decapod species; they consist of typical secretory cells with drainage canals (intercellular ducts) leading into a central collecting canal and a main duct leading to the surface.

A function in stabilising the burrow wall has been suggested by Thompson (1972) for certain glands. She employed several methods to demonstrate that the secretions of the hindgut gland are used to plaster the burrow wall in *Upogebia pugettensis* (Dana 1852), but could not exclude that secretions of the appendages, especially the mxp3, may contribute as well. In *Upogebia*, burrowing behaviour includes a somersault with a turn around the long axis in which the material carried in the basket comes into contact with the dorsal side of the telson. Such a somersault is not obligatory in species of *Callianassa*.

Rodrigues & Hödl (1990) report that *Sergio mirim* (Rodrigues 1971) coats the walls of its burrow with a sticky secretion visible as threads of mucus-like secretions on the ventral side of the abdomen and that *Callichirus major* (Say 1818) smoothens the wall during the cementing process with the trowel-like propodus of P3. In addition, the animal is often observed to rub the dorsal side of its abdomen along the burrow wall.

Manning & Felder (1987) suggest that the dorsal plates on the abdominal segments which are typical for the genus *Callichirus* (*s. str.*) may belong to a glandular system; accordingly, this system plays a role in plastering the burrow wall of these species, which inhabit very unstable beach sediments.

Further studies are necessary to determine the chemical nature of the secretions produced by the glands, the detailed mechanism of incorporation into the burrow wall, the fate of this material within the burrow wall sediment, and its influence on burrow wall chemistry.

Conclusions

Appendages of *Callianassa candida* and *Callianassa tyrrhena* involved in manipulating the burrow wall are nearly filled with "rosette glands". At the appendage surface these glands open via pores with emanating mucus threads. Mucus threads are also visible between sediment grains of the burrow wall. The secretions of the glands are obviously incorporated into the burrow wall sediment in order to used to stabilise it.

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