

# Adhesion in echinoderms

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## CONTENTS

- 1 Introduction
  - 2 The podia
    - 2.1 Diversity
    - 2.2 Basic structure and function
    - 2.3 Adhesivity
  - 3 Other attachment mechanisms of echinoderms
    - 3.1 Larval and postlarval adhesive structures
    - 3.2 Cuvierian tubules
  - 4 Comparison with other marine invertebrates
  - 5 Conclusions and prospects
- Acknowledgements  
References

## 1 INTRODUCTION

Marine organisms have developed a wide range of mechanisms allowing them to attach to or manipulate a substratum (Nachtigall 1974). Among these mechanisms, one can distinguish between mechanical attachments (e.g. hooks or suckers) and chemical attachments (with adhesive substances).

The phylum Echinodermata is quite exceptional in that all its species,

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whatever their life style, use attachment mechanisms. These mechanisms allow some of them to move, others to feed, and others to burrow in particulate substrata. In echinoderms, adhesivity is usually the function of specialized structures, the podia or tube-feet. These podia are the external appendages of the ambulacral system and are also probably the most advanced hydraulic structures in the animal kingdom.

## 2 THE PODIA

From their presumed origin as simple respiratory evaginations of the ambulacral system (Nichols 1962), podia have diversified into the wide range of specialized structures found in extant echinoderms. This morphological diversity of form reflects the variety of functions that podia perform (Lawrence 1987). Indeed, they take part in locomotion, burrowing, feeding, sensory perception and respiration. In some groups, a single type of podium fulfils different functions; in others, different types of podia coexist each with their own function.

### 2.1 Diversity

Based on their external morphology only, echinoderm podia can be divided into six broad types: disc-ending, penicillate, knob-ending, lamellate, ramified, and digitate (Table 1, Plates 1.1-1.4 and 2.1-2.4).

*Disc-ending podia* consist of a basal extensible cylinder, the stem, with an apical extremity which is enlarged and flattened to form the so-called disc (Plate 1.1). They are found in asteroids, echinoids and holothuroids. In the latter two classes, the disc encloses a supportive skeleton made up of an association of large (the ossicles) and small (the spicules) calcareous plates.

Most podia of regular echinoids, asteroids (except members of the order Paxillosida), and dendrochirote and aspidochirote holothuroids end with a disc. They are involved in locomotion and attachment, the disc being the site of contact with the substratum (J.E. Smith 1937, 1947, Nichols 1961, A.B. Smith 1978).

Peristomeal podia of regular echinoids do not take part in locomotion and attachment; yet they are also disc-ending. These podia are sensory and presumably test the 'edibility' of detritic materials before they are ingested (Nichols 1961, A.B. Smith 1979). They also function in consolidating food particles or food fragments in an adhesive material, thus facilitating their ingestion by the Aristotle's lantern (Flammang & Jangoux 1993).

Disc-ending podia also occur in sand-dollars (irregular echinoids, order Clypeasteroidea). In these echinoids, which are psammivores, podia are involved in feeding. Their minute size allows them to handle individual sand grains (Nichols 1959b, Mooi 1986a,b).

*Penicillate podia* are derived from disc-ending podia (A.B. Smith 1980). They have the same basic structure but their disc bears numerous digitations (Plate 1.2). These digitations may either cover the whole disc surface or are limited to its margin. Each digitation is supported by a calcareous rod. All the rods together are homologous to the skeleton of disc-ending podia (A.B. Smith 1980).

These podia occur exclusively in irregular echinoids of the order Spatangoida. Spatangoid echinoids live in a burrow in the sediment and use their penicillate podia for different functions. The podia surrounding the mouth are involved in feeding (they collect particles on the floor of the burrow and bring them to the mouth). The others, located at the posterior and on the top of the animal, build and maintain extensions of the burrow (Nichols 1959a, A.B. Smith 1980, Flammang et al. 1990).

*Knob-ending podia* are made up of a basal cylindrical stem ending apically with a rounded knob (Plates 1.3 and 1.4). Many echinoderm groups possess such podia and the functions they fulfil are varied. As in disc-ending podia, there may be a supportive calcareous skeleton in the knob of echinoid and holothuroid podia, but this is not always the case.

In diadematooid and arbaciooid echinoids, aboral podia are knob-ending and involved mainly in respiration (Fenner 1973, A.B. Smith 1978). In these podia, the knob is very much reduced and lacks any skeletal framework. Peristomeal podia of cidaroid and echinothurioid echinoids also end in knobs and are sensory ('gustatory') in function (Nichols 1961, A.B. Smith 1979). Knob-ending podia are also found around the ambitus in spatangoid echinoids and are sensory (Plate 1.3) (Nichols 1959a, A.B. Smith 1980). These podia lack any skeleton.

In asteroids, there are knob-ending podia at the tip of each arm. These podia, always in motion, are chemosensory (Sloan & Campbell 1982). Paxillosid asteroids, which are found on particulate substrata, possess these sensory podia. Their other podia also end in knobs but are larger and more conical in shape (Plate 1.4). They take part in locomotion and burrowing (Heddle 1967, Engster & Brown 1972).

Aspidochirote holothuroids possess knob-ending podia too. In these animals, these so-called papillae are located dorsally and are sensory in function (VandenSpiegel et al. 1995).

Lastly, the podia of many ophiuroids end in knobs. These podia, located on the oral surface of each arm, may be involved in locomotion,

Table 1. Shape, location and function of echinoderm podia.

Taxon		Shape	Location	Function	Illustration	References	
Class	Order*						
Echinoidea	Cidaroida and Echinothurioida	Lamellate	Aboral surface of the test	Respiration	Pl. 1.1	Nichols 1961, Fenner 1973, A.B. Smith 1978, 1979	
		Knob-ending	Around the mouth	Sensory perception			
		Disk-ending	Oral surface of the test	Locomotion, attachment			
	Diadematoidea and Arbacioidea	Knob-ending	Aboral surface of the test	Respiration			Fenner 1973, A.B. Smith 1978, 1979
		Disk-ending	Oral surface of the test	Locomotion, attachment			
	Temnopleuroidea and Echinoida	Disk-ending	Around the mouth	Sensory perception			Nichols 1961, A.B. Smith 1978, 1979, Flammang & Jangoux 1993
			Aboral and oral surfaces of the test	Locomotion, attachment, respiration			
	Clypeasteroida	Lamellate	Aboral surface of the test	Respiration			Fenner 1973, A.B. Smith 1980, Mooi 1986b
		Disk-ending	Aboral and oral surfaces of the test	Feeding, sensory perception			
	Spatangoida	Lamellate	Aboral surface of the test	Respiration			Pl. 2.1
Knob-ending			Ambitus	Pl. 1.3			
Penicillate			Around the mouth	Pl. 1.2			
			Inside the internal and subanal fascioles	Burrowing			
Asteroidea	Paxillosida	Knob-ending	Oral surface of the arms	Locomotion, burrowing	Pl. 1.4	Nichols 1966, Sloan & Campbell 1982	
	Valvatida, Spinulosida and Forcipulatida	Disk-ending	Oral surface of the arms	Sensory perception			
		Knob-ending	Arm tips	Locomotion, attachment			
			Arm tips	Sensory perception		Sloan & Campbell 1982	

Table 1. (Continued).

Taxon		Shape	Location	Function	Illustration	References
Class	Order*					
Holothuroidea	Dendrochirotida	Disk-ending Ramified	Along the body (5 rows) Around the mouth	Locomotion, attachment Feeding, sensory perception		J.E. Smith 1937, Massin 1982
	Aspidochirotida	Disk-ending Knob-ending Ramified	Ventral surface (trivium) Dorsal surface (bivium) Around the mouth	Locomotion, attachment Sensory perception Feeding, sensory perception		J.E. Smith 1937, Massin 1982, Vanden Spiegel et al. 1995
	Apodida	Ramified	Around the mouth	Feeding, sensory perception	Pl. 2.2	Massin 1982
Ophiuroidea		Knob-ending or digitate	Oral surface of the arms	Feeding, burrowing, locomotion, attachment, respiration, sensory perception	Pl. 2.3	Woodley 1967, Warner 1982
Crinoidea		Digitate	Oral surface of the arms and pinnules	Feeding, respiration, sensory perception	Pl. 2.4	Nichols 1960, Byrne & Fontaine 1983, Lahaie & Jangoux 1985

\*Only the main orders have been considered.

burrowing or feeding, depending on the species (Woodley 1967, Pentreath 1970, Warner 1982).

*Lamellate podia* are knob-ending podia with a very developed and flattened stem (Plate 2.1). The stem also is usually very folded, looking like a pile of lamellae, hence their name.

These podia may be found in cidaroid and echinothurioid echinoids as well as in irregular echinoids. Always located on the aboral surface of the echinoid, they are more or less elongated and/or folded according to the species considered. They are respiratory in function (Fenner 1973, A.B. Smith 1978, 1980).

*Ramified podia* are made up of a central cylindrical stem bearing lateral branches that may again divide into smaller units. The whole podium (stem and lateral branches) may enclose supportive spicules.

These podia, the so-called buccal tentacles, are characteristic of holothuroids. Always located around the mouth, they are the food-collecting structures of these animals. According to the feeding habits (suspension-feeding or deposit-feeding) of the holothuroids, ramified podia are dendritic, peltate or pinnate (Plate 2.2). However, all behave in the same way: the tentacle extends and its branches catch food particles either in the water column or on or in the substratum. The podium then bends and enters the mouth where it releases its load (Massin 1982).

*Digitate podia* are cylindrical with a slender tip and occur in ophiuroids and crinoids (Plates 2.3 and 2.4).

In ophiuroids, they may or may not be covered with small papillae (Pentreath 1970). Depending on the species, they function in locomotion or burrowing, or in feeding by catching food particles and/or transporting them to the mouth (Woodley 1967, Pentreath 1970, Warner 1982). In crinoids, digitate podia are always covered with small papillae. Triplets of podia of different sizes are used in catching food particles in the water column (Nichols 1960, Byrne & Fontaine 1983, Lahaye & Jangoux 1985).

## 2.2 Basic structure and function

### 2.2.1 Structure

Whatever the echinoderm species, the histological structure of podia is remarkably constant. They consist of four tissue layers (Fig. 1): an inner and an outer epithelium, with a connective tissue layer and a nerve plexus sandwiched between them (Kawaguti 1964, Nichols 1966, Florey &

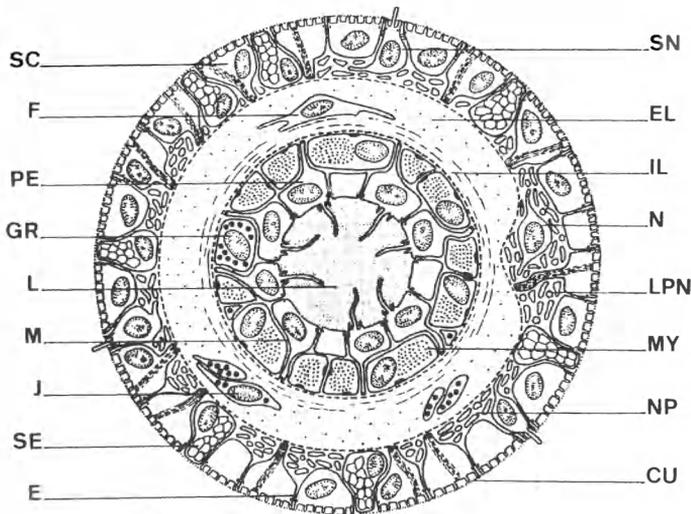
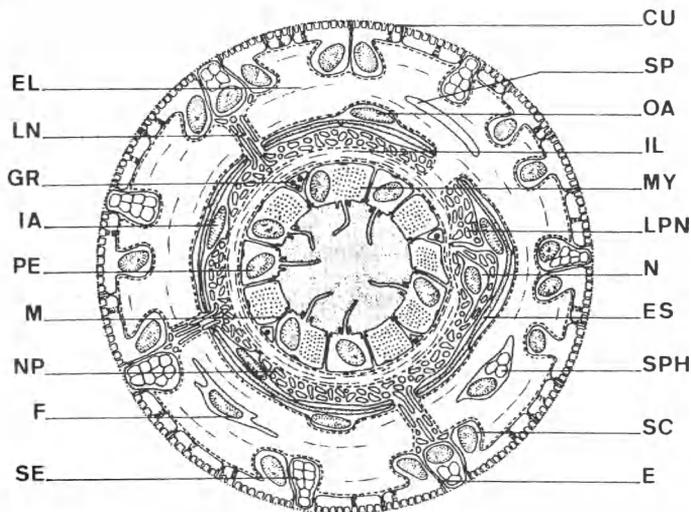
**A****B**

Figure 1. Reconstruction of transverse sections through the stem of typical echinoid (A) and holothuroid (B) podia (original, not to scale). CU = cuticle, E = epidermis, EL = connective tissue sheath external layer, ES = epineural sinus, F = fibrocyte, GR = granulocyte, IA = inner adsinusal cell, IL = connective tissue sheath internal layer, J = juxtaglignamental-like cell, L = ambulacral lumen, LN = lateral nerve, LPN = longitudinal podial nerve, M = mesothelium, MY = myocyte, N = neurone body, NP = nerve plexus, OA = outer adsinusal cell, PE = peritoneocyte, SC = support cell, SE = secretory cell, SN = sensory cell, SP = spicule, SPH = spherulocyte.

Cahill 1977, Flammang & Jangoux 1992a). The inner epithelium, viz. the mesothelium, is continuous with that lining the inner parts of the ambulacral system whereas the outer epithelium, viz. the epidermis, is continuous with that covering the rest of the body. It is mainly this last layer which is highly specialized in the various types of podia, chiefly with respect to the secretory cells situated in it.

*The mesothelium* (coelomic epithelium) lines the podium lumen (Fig. 1). It is a myoepithelium comprising two main cell types: peritoneocytes and myocytes that both contact the underlying basal lamina to which they attach via hemidesmosomes (Wood & Cavey 1981, Rieger & Lombardi 1987, Cavey & Wood 1991). Peritoneocytes are monociliated cells bearing a long vibratile cilium surrounded by a ring of about ten microvilli. They enclose a bundle of filaments connecting their apical and basal membranes (Wood & Cavey 1981). Myocytes contain a bundle of myofibrils associated with numerous mitochondria. These myofibrils are oriented longitudinally. Together they form an extensive longitudinal muscle layer (viz. the retractor muscle of the podium) (Wood & Cavey 1981). Adjacent myocytes are connected by spot desmosomes (Wood & Cavey 1981, Rieger & Lombardi 1987).

In the podia of most echinoderms, the mesothelium is organized as a pseudostratified epithelium consisting of apically situated peritoneocytes (adluminal cells) and subapical myocytes (Fig. 1A) (Florey & Cahill 1977, Wood & Cavey 1981, Rieger & Lombardi 1987, Cavey & Wood 1991, Flammang & Jangoux 1992a). However, in the podia of crinoids and ophiuroids, and in the buccal tentacles of some holothuroids, the mesothelium is a simple epithelium, both peritoneocytes and myocytes contributing to the adluminal surface of the mesothelium (Fig. 1B) (Martinez 1977d, Bouland et al. 1982, Cameron & Fankboner 1984, Rieger & Lombardi 1987). In both cases, adluminal cells (i.e. peritoneocytes only in pseudostratified mesothelia; peritoneocytes and myocytes in simple mesothelia) are connected apico-laterally by junctional complexes consisting of a distal zonula adhaerens and a proximal septate desmosome (Wood & Cavey 1981, Rieger & Lombardi 1987).

An additional cell type may be found in the mesothelium of echinoderm podia, viz. the granulocytes. However, these are much less common than peritoneocytes and myocytes (Wood & Cavey 1981, Rieger & Lombardi 1987). So far, their function remains obscure.

Contrary to the arrangement in the mesothelium lining the perivisceral coelom, there is no nerve plexus associated with the mesothelium of the podia (Florey & Cahill 1977, Cobb 1987).

*The connective tissue sheath* is made up of an amorphous ground substance that encloses bundles of collagen fibrils (i.e. fibers), elongated cells with an electron-dense cytoplasm which may be fibrocytes, and various types of mesenchymal cells (macrophages, spherulocytes, etc.) (Kawaguti 1964, Nichols 1966, Florey & Cahill 1977, Martinez 1977b, Flammang & Jangoux 1992a).

The connective tissue sheath generally consists of a diffuse external layer and a more compact internal layer (Fig. 1). However, in crinoids, some ophiuroids, and a few species of clypeasteroid echinoids, only the internal layer is present (Nichols 1959b, 1960, Woodley 1967, 1980). Within the internal layer, the collagen fibers are generally said to be circular in arrangement (J.E. Smith 1947, Nichols 1961, 1966, Kawaguti 1964, Perpeet & Jangoux 1973, Martinez 1977b, Florey & Cahill 1977, Mooi 1986a). On the contrary Woodley (1980) and Skyler McCurley & Kier (1995) described the connective internal layer as a crossed-fiber helical array of collagen fibers. According to these authors, this crossed-fiber helical connective tissue layer in retracted podia may sometimes give the misleading impression that it consists of circular fibers. In echinoids, asteroids and ophiuroids, the external layer has fibers oriented longitudinally (Fig. 1A) (Nichols 1961, 1966, Kawaguti 1964, Perpeet & Jangoux 1973, Martinez 1977b, Florey & Cahill 1977), and also contains cells which enclose numerous electron-dense granules which are strikingly similar in appearance to the juxtaligamental cells of mutable connective tissues (see the review of Wilkie 1996). In holothuroids, on the other hand, the collagen fibers of the external layer are oriented circularly (or helically?) (Fig. 9B) (Bouland et al. 1982, Flammang & Jangoux 1992a).

In echinoids and holothuroids, the external connective layer may contain one or several kinds of embedded calcareous spicules (Fig. 1B) (Nichols 1966, A.B. Smith 1978, Cameron & Fankboner 1984, Flammang & Jangoux 1992a, 1993, VandenSpiegel et al. 1995).

*The nerve plexus* is a cylindrical sheath of ectoneural nervous tissue (Cobb 1987). In most species, it is located just beneath the epidermis, its neurites running between the basal parts of epidermal cells (Fig. 1A) (Kawaguti 1964, Nichols 1966, Florey & Cahill 1977). In holothuroids and some ophiuroids it is located deeper in the connective tissue external layer and sends small lateral nerves to innervate the epidermis (Fig. 1B) (Martinez 1977c, Bouland et al. 1982, McKenzie 1987, 1988a, Flammang & Jangoux 1992, Byrne 1994). In both cases, however, a single continuous basal lamina lines both the epidermis and the nerve plexus, separating them from the connective tissue.

The plexus is thickened on one side of the podium to form the longi-

tudinal nerve, and also, generally, at the proximal and distal extremities to form two nerve rings (Nichols 1966). It is also always well-developed at the level of the secretory and/or sensory areas of the podial epidermis. Nerve cell bodies occur in the longitudinal podial nerve, in the nerve rings, as well as in areas where the plexus is thickened; the rest of the plexus consists of a criss-cross of nerve processes. The latter contain mitochondria, microtubules, and clear and/or dense-core vesicles. Numerous vesiculated nerve terminals are found on the basal lamina separating the nerve plexus from the connective tissue sheath (Florey & Cahill 1977).

In holothuroid podia, the outer face of the nerve plexus is adjacent to a narrow cavity, viz. the epineural sinus, which is lined by highly flattened adsinusal cells (Fig. 1B) (Flammang & Jangoux 1992, VandenSpiegel et al. 1995). The outer adsinusal cells are highly flattened (1.5  $\mu\text{m}$  thick at the most); they rest upon the outer basal lamina of the nerve plexus. The inner adsinusal cells rest upon the nerve plexus itself; they send basal filament-containing processes that traverse the nerve plexus before contacting its inner basal lamina. Adsinusal cells bear a single cilium that extends into the nerve sinus.

*The epidermis*, which is a monostratified epithelium, covers the podium externally (Fig. 1). It may enclose different cell types: support cells, sensory cells, and secretory cells (Holland 1984). The latter two are particularly abundant in the epidermal adhesive areas of the podia (see below). All epidermal cells are connected apico-laterally by junctional complexes made up of a distal zonula adhaerens and a proximal septate desmosome. In general, support cells are the most numerous and form a supportive meshwork in which the other cell types are homogeneously distributed. The epidermis is coated by a well-developed, multi-layered glycocalyx, the so-called cuticle (Holland 1984).

Support cells are traversed by a bundle of filaments joining their apical and basal membranes. According to Harris & Shaw (1984), this bundle is made up of intermediate filaments. The apical cytoplasm always includes 'empty' vesicles and vacuoles of diverse sizes. At the apex of support cells, there are numerous branched and unbranched microvilli that are closely associated with fibrous and/or granular materials constituting the cuticle. In addition to their supportive function, support cells also are presumably involved in uptake of dissolved organic material and in cuticular material synthesis (Engster & Brown 1972, Souza Santos & Silva Sasso 1974). In holothuroids, connective tissue protrusions insinuate themselves between the nucleus-containing cell bodies of the support cells, which gives them a *T*-shaped aspect in section (Fig. 1B). Their bundle of filaments is located in the narrow lateral cell processes.

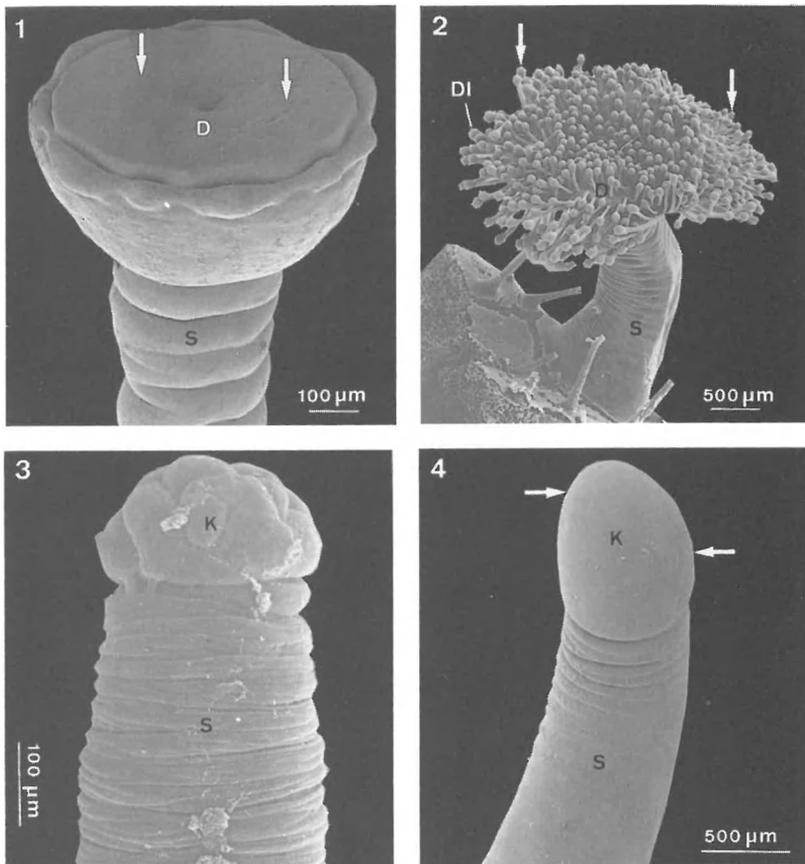


Plate 1. External morphology of echinoderm podia (arrows indicate the location of epidermal adhesive areas). 1) Disc-ending podium of the echinoid *Sphaerechinus granularis* (from Flammang & Jangoux 1993). 2) Peribuccal penicillate podium of the echinoid *Echinocardium cordatum* (from Flammang et al. 1991). 3) Knob-ending podium of the echinoid *Echinocardium cordatum* (original). 4) Locomotory knob-ending podium of the asteroid *Luidia maculata* (from Flammang 1995). D = disc, DI = digitation, K = knob, S = stem.

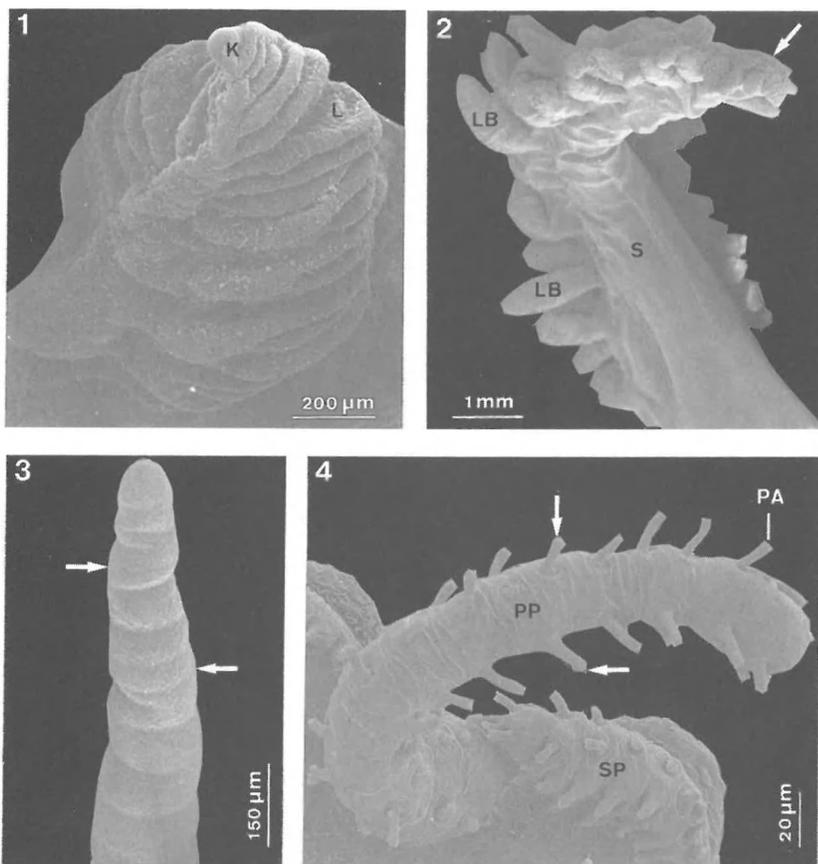


Plate 2. External morphology of echinoderm podia (continued) (arrows indicate the location of epidermal adhesive areas). 1) Lamellate podium of the echinoid *Echinocardium cordatum* (original). 2) Pinnate ramified podium (buccal tentacle) of the holothuroid *Synapta maculata* (original). 3) Digitate podium of the ophiuroid *Asteroonyx loveni* (original). 4) Digitate podia of the crinoid *Antedon bifida* (from Flammang & Jangoux 1992b). K = knob, L = lamella, LB = lateral branch, PA = papilla, PP = primary podium, S = stem, SP = secondary podium.

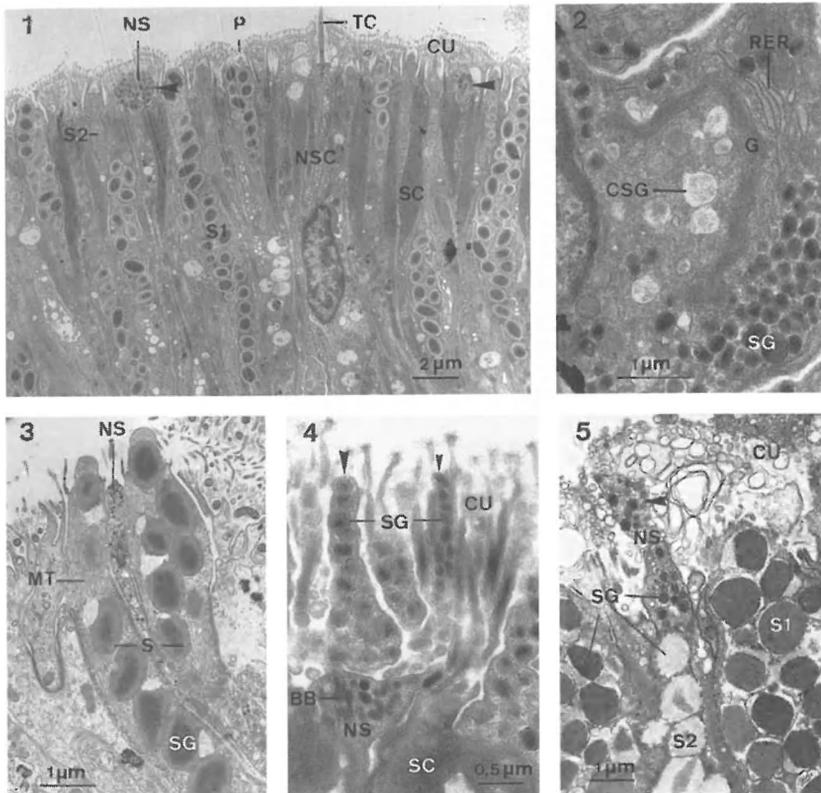


Plate 3. Ultrastructure of echinoderm podial adhesive systems. 1) Longitudinal section through the apex of the disc epidermis in the asteroid *Marthasterias glacialis* (arrowheads indicate the apical bulge of neurosecretory-like cells) (original). 2) Detailed view of the cell body of a secretory cell in the echinoid *Sphaerechinus granularis* (from Flammang & Jangoux 1993). 3) Longitudinal section through a sensory-secretory complex showing a neurosecretory-like cell flanked by two secretory cells in the ophiuroid *Asteronyx loveni* (original). 4) Surface of the adhesive epidermis in *S. granularis* (arrowheads indicate microvillar-like cell projections of a secretory cell (large one) and of a neurosecretory-like cell (small one)) (original). 5) Apex of a neurosecretory-like cell in the asteroid *Luidia ciliaris* (arrowhead indicates the apical bulge of the neurosecretory-like cell) (from Flammang 1995). BB = basal body, BF = bundle of filaments, BL = basal lamina, CSG = condensing secretory granule, CTP = connective tissue protrusion, CU = cuticle, G = Golgi apparatus, MT = microtubules, NP = nerve plexus, NS = neurosecretory-like cell, NSC = sensory cell, P = pore, RER = rough endoplasmic reticulum cisternae, S = secretory cell, S1 = Type 1 secretory cell, S2 = Type 2 secretory cell, SC = support cell, SG = secretory granule, TC = transcuticular cilium.

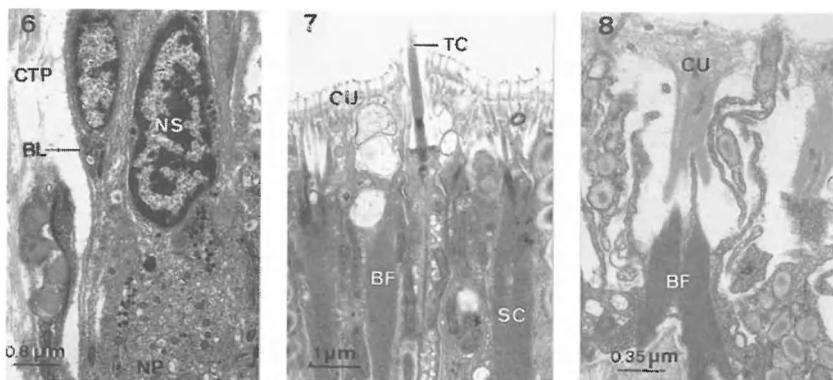


Plate 3. (Continued). 6) Basal part of a neurosecretory-like cell in the holothuroid *Holothuria forskali* (from Flammang & Jangoux 1992a). 7) Apex of a sensory cell in *M. glacialis* (from Flammang et al. 1994). 8) Support cell of *H. forskali* (from Flammang & Jangoux 1992a). BB = basal body, BF = bundle of filaments, BL = basal lamina, CSG = condensing secretory granule, CTP = connective tissue protrusion, CU = cuticle, G = Golgi apparatus, MT = microtubules, NP = nerve plexus, NS = neurosecretory-like cell, NSC = sensory cell, P = pore, RER = rough endoplasmic reticulum cisternae, S = secretory cell, S1 = Type 1 secretory cell, S2 = Type 2 secretory cell, SC = support cell, SG = secretory granule, TC = transcuticular cilium.

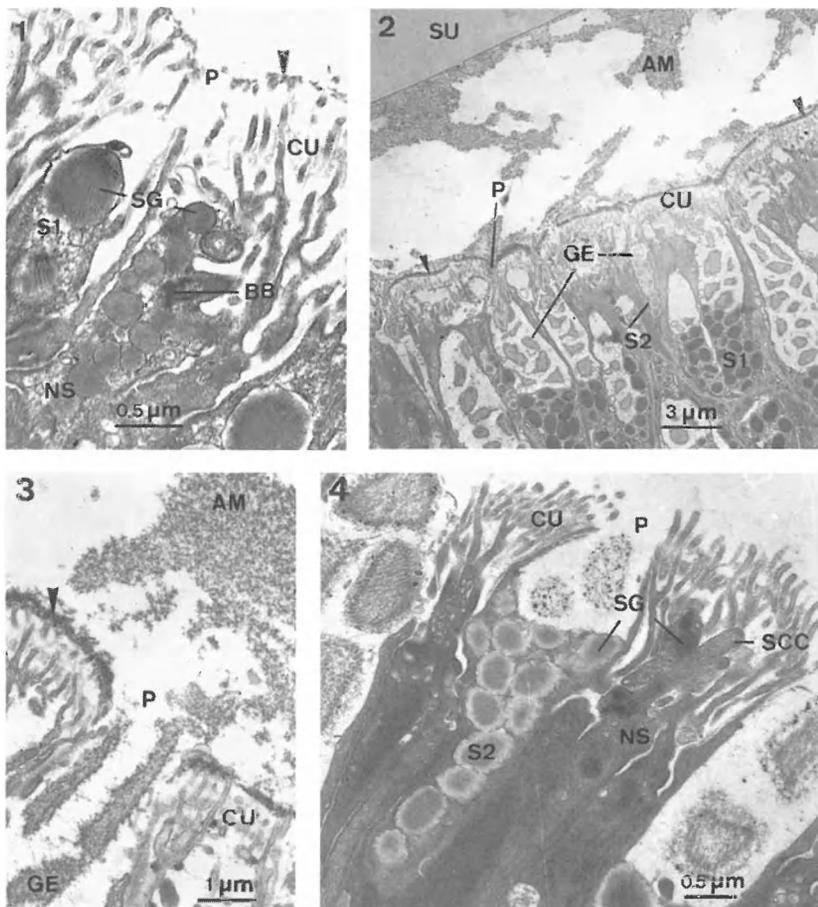


Plate 4. Ultrastructure of the podial adhesive system in the asteroid *Asterias rubens* before attachment, during attachment and after detachment (arrow heads indicate the fuzzy coat). 1) Apex of the adhesive epidermis before attachment (original). 2) Epidermis of an attached podium (from Flammang et al. 1994). 3) Detailed view of the apex of a secretory cell in an attached podium (from Flammang et al. 1994). 4) Apex of the adhesive epidermis after detachment (compare with Plate 4.1, original). AM = adhesive material, BB = basal body, CU = cuticle, GE = granules in the process of extrusion, NS = neurosecretory-like cell, P = pore, S1 = Type 1 secretory cell, S2 = Type 2 secretory cell, SCC = subcuticular cilium, SG = secretory granules, SU = substratum.

Sensory cells are usually scattered singly or in small groups. They are characterized by a basally produced axon and bear a single short apical cilium arising from a basal body associated to a long ciliary rootlet. It is generally assumed that such cells are chemoreceptors or mechanoreceptors (Cobb & Moore 1986, Cobb 1987).

Secretory cells may be scattered individually or aggregated into small or large groups. Their predominant cytoplasmic inclusions are membrane-bound secretory granules. Each podium possesses generally three to six different types of secretory cells, each having typically only one kind of secretory granule (Martinez 1977a, Holland 1984, Flammang & Jangoux 1992a, 1993). These different cell types may be characteristic of different areas of the podial epidermis. Although some are known to be involved in the adhesive process (see below), the function of the others is in general poorly understood.

### 2.2.2 Function

The operation of podia is generally regarded as the *raison d'être* of the ambulacral system (Nichols 1966). Podia are hydraulic structures and, for their correct functioning, they must contain a fluid maintained at a sufficient hydrostatic pressure. The circumoral canal and the radial canals deliver the ambulacral fluid to all podia, the Polian vesicles being used as reservoirs for this fluid (Nichols 1966, 1972). The hydrostatic pressure is generated by the hyperosmolarity of the ambulacral fluid that causes water to come in through the wall of the ambulacral system (Prusch & Whoriskey 1976, Ferguson 1990).

Echinoderm podia may take part in respiration, sensory perception, locomotion, attachment, feeding, or burrowing. All podia are probably involved in respiration by taking advantage of the proximity of the external medium to a body fluid. Only echinoids possess lamellate podia that are exclusively respiratory, but respiratory exchanges at the level of the podia is also important in echinoderms that do not have specialized respiratory structures, i.e. the ophiuroids and the crinoids. Echinoid lamellate podia are adapted for respiratory exchanges in different ways: 1) they are positioned favourably on the animal, 2) their surface area is increased by flattening and folding, 3) the thickness of their wall is greatly reduced through loss of the retractor muscle and decrease in the thickness of the connective tissue layer, and 4) there is a separation of ciliary currents in the podial lumen due to the double pore at the base of the podium and to the presence of a septum within the lumen (Fenner 1973).

Only some knob-ending podia are exclusively sensory in function. The epidermis of their knob forms a specialized area in which ciliated sensory cells are particularly numerous (Nichols 1959a, VandenSpiegel et al. 1995, Flammang unpubl. obs.). At this level, there is also an impor-

tant development of the nerve plexus. These podia presumably are involved in chemo- and/or mechanoreception. It is important to remember that all other podia, although they are not exclusively sensory in function, have important sensory abilities. Indeed, they all possess epidermal sensory cells either associated with the epidermal adhesive areas or simply scattered all over the surface of the podium.

Locomotion, attachment, feeding, and burrowing are functions that require the formation of an adhesive bond between the podium and a substratum and a great mobility of the podia. Attachment is achieved by specialized adhesive areas that are always located at the level of functionally important parts of the podia. The fine structure of the adhesive areas and the functioning of the adhesive process will be discussed in detail in Section 2.3.

The mobility of echinoderm podia can be explained by combinations of three basic movements: protraction, flexion and retraction, which result from the antagonistic action of the ambulacral fluid hydrostatic pressure and the podial retractor muscle (Nichols 1966). For a podium to extend, a force must be exerted that pushes the ambulacral fluid into its lumen. In crinoids and ophiuroids, this force is produced by the contraction of sections of the radial canal while, in asteroids, echinoids and holothuroids, the protraction of the podium is brought about by the contraction of a small muscular sac, the ampulla (Nichols 1966, 1972, Woodley 1980, Skyler McCurley & Kier 1995). Each podium-ampulla unit is separated from the lateral and radial canals by a valve that prevents the enclosed fluid from escaping into the lateral canal when the ampulla contracts. The elongation process is made possible by the properties of the podial connective tissue sheath. Within this sheath, the internal layer prevents the podial wall from being bent out of shape and maintains the diameter of the podium so that the whole hydrostatic pressure is exerted at its distal end (Woodley 1980, Skyler McCurley & Kier 1995), while the external layer, which may have mutable properties (Byrne 1994), stretches to allow the podium to lengthen. Interestingly, an external layer enclosing longitudinal collagen fibers and juxtaligamental-like cells is only observed in podia that have great capacities of elongation, i.e. echinoid, asteroid and ophiuroid podia. The podia in the other classes rely mostly on flexion movements to operate. Retraction is brought about by the contraction of the podial retractor muscle. The ambulacral fluid is then driven back into the radial canal or into the ampulla according to the groups. The retractor muscle is also involved in bending the podium in one direction or another. It seems that each sector of the muscular cylinder can contract independently from the others and therefore act on the hydraulic skeleton to produce flexion. How such fine control of the contraction of the myocytes is achieved is still poorly understood, since there

is no direct innervation of the retractor muscle. Instead, it appears that innervation takes place through the release of neurotransmitters from the nerve terminals attached to the internal basal lamina of the nerve plexus. These neurotransmitters then have to diffuse across the whole depth of the connective tissue sheath before reaching the myocytes of the mesothelium (Florey & Cahill 1977).

## 2.3 Adhesivity

Although a few podia are exclusively sensory or respiratory, most are involved in locomotion, attachment, feeding or burrowing, that require the formation of an adhesive bond between the podium and a substratum. These different functions can be divided into two broad categories: those requiring the podia to rest on the sea-bottom (e.g. locomotion or attachment) and those requiring the podia to handle particles (e.g. feeding or burrowing).

Adhesive mechanisms involve mechanical and chemical attachments. The latter is the main adhesive strategy of extant echinoderms. Indeed, all podia, both locomotory and handling, use chemical attachment to fulfil their function. In penicillate podia, knob-ending podia, ramified podia, and digitate podia, only chemical attachment is involved. Disc-ending podia, however, can use a combination of both chemical and mechanical attachments.

### 2.3.1 Chemical attachment

Chemical adhesion is the result of secretory activity by the adhesive areas of the podia. Podial secretions have been the subject of a large number of investigations using both light and electron microscopy, but their composition and mode of operation are still poorly understood. Adhesion has long been considered the result of 'mucus' secretion (J.E. Smith 1937); an opinion that has then been followed by most authors. Hermans (1983) proposed a more elaborate model for echinoderm podial adhesion. In his hypothesis, podia possess duo-gland adhesive systems involving two types of secretory cells, viz. cells releasing an adhesive secretion and cells releasing a de-adhesive secretion. However according to McKenzie (1988b), morphological observations supporting such adhesive systems were rare, and more ultrastructural studies of echinoderm podia were needed.

2.3.1.1 *Comparative ultrastructure of podial adhesive areas.* Light microscopy studies on echinoderm species have shown specialized glandular areas, the adhesive areas, in the epidermis of the podia. These areas are always located at the level of functionally important parts of the po-

dia, such as the disc surface in disc-ending podia (Plate 1.1) (J.E. Smith 1937, Nichols 1959b, 1961, Perpeet & Jangoux 1973), the distal surface of the disc and/or of the digitations in penicillate podia (Plate 1.2) (Nichols 1959a), the surface of the knob in knob-ending podia (Plate 1.4) (Engster & Brown 1972), the apex of the ramifications or the whole aboral surface (Plate 2.2) in ramified podia (Bouland et al. 1982, McKenzie 1987), and the whole surface (Plate 2.3) or the papillae (Plate 2.4) in digitate podia (Nichols 1960, Pentreath 1970).

As a general rule, epidermal adhesive areas of echinoderm podia always consist of four cell categories (Table 2; Fig. 2): secretory cells of one or two types, neurosecretory-like cells, sensory cells, and support cells. All of these cells are connected apically by junctional complexes made up of a distal zonula adhaerens and a proximal septate desmosome. Externally, the epidermis is covered by a multi-layered glycocalyx, the cuticle.

*Secretory cells* are generally flask-shaped. Their enlarged cell bodies are located basally and attach to the basal lamina via hemidesmosomes. Each cell body sends out a long apical process that reaches the surface of the podium. The cytoplasm of both the cell body and the apical process is filled with membrane bound secretory granules (Fig. 2, Plates 3.1-3.5).

Granules are usually made up of at least two materials of different electron density which gives them a complex ultrastructure varying from one taxon to another. Five broad groups can be recognized (Table 2): 1) homogeneous granules apparently made up of only one material, 2) heterogeneous granules in which two different materials are mixed in an irregular pattern, 3) dense-cored granules consisting of an electron-denser core surrounded by less dense material, 4) granules with a central filamentous bundle resembling granules of the previous group but in which the core is made up of a parallel arrangement of fibrils or rods, and 5) capped granules in which an electron-luscent material is covered, on one side, by a cap of electron-dense material. These differences in the secretory granules probably depend upon the nature of their contents.

In the cell body of secretory cells, developing granules are closely associated with Golgi membranes and rough endoplasmic reticulum cisternae (Fig. 2, Plate 3.2). This suggests that these organelles are involved in the synthesis of the granule contents (e.g. Harrison & Philpott 1966, Harrison 1968, Engster & Brown 1972, Flammang & Jangoux 1993). Granules are then conveyed to the apex of the cell probably with the help of the longitudinal microtubules occurring in the secretory cell distal process (Fig. 2, Plate 3.3). Two modes of granule secretion can be recognized according to the morphology of the apex of the secretory cell (see also McKenzie 1988b, Flammang & Jangoux 1992a). In one, in

'apical duct' cells, secretory granules are extruded through a duct delimited by a ring of microvilli and opening onto the podial surface as a cuticular pore (Fig. 2A, Plates 3.1 and 3.3). This kind of secretory cell occurs in holothuroid locomotory podia and in ophiuroid and asteroid podia. In the other, in 'apical tuft' cells, secretory granules are released at the tip of microvillar-like cell projections which are arranged in a tuft at the cell apex (Fig. 2B, Plate 3.4). This second kind of secretory cell has been observed only in echinoid podia and holothuroid locomotory podia and buccal tentacles.

*Neurosecretory-like cells* are generally less obtrusive than secretory cells in TEM sections (especially in locomotory podia). This is probably the reason why some workers failed to recognize them (Table 2). These cells are narrow and have a centrally-located nucleus. They are filled with small electron-dense secretory granules (Fig. 2, Plates 3.4-3.6). The cytoplasm of neurosecretory-like cells also contains numerous RER cisternae, a small Golgi apparatus and longitudinally arranged microtubules. At the apex of neurosecretory-like cells from echinoid, holothuroid and ophiuroid podia, the secretory granules have been observed in microvillar-like cell projections ending apically at the surface of the podia (Fig. 2B, Plate 3.4) (McKenzie 1987, Ball & Jangoux 1990, Flammang et al. 1991, Flammang & Jangoux 1992a, 1993, 1994). In asteroid podia, the granules occur apically in a large cell bulge (Fig. 2A, Plates 3.1, 3.5 and 4.1) (Flammang et al. 1994, Flammang 1995). The basal end of neurosecretory-like cells is tapered and penetrates the nerve plexus (Plate 3.6) while their apex usually bears a short subcuticular cilium which sometimes presents an irregular arrangement of the microtubules (Fig. 2, Plates 4.1 and 4.4) (see e.g., Ball & Jangoux 1990, Flammang & Jangoux 1992a). These cilia were not found, however, in the cells of clypeasteroid echinoid and paxillosid asteroid podia and in those of holothuroid tentacles (T.B. Smith 1983, McKenzie 1987, 1988a, Flammang & Jangoux 1994, Flammang 1995).

*Sensory cells* have the same shape as neurosecretory-like cells. Their cytoplasm encloses longitudinally arranged microtubules, elongated mitochondria, and small apical vesicles. These cells are characterized by a single short cilium (Fig. 2, Plate 3.7) whose apex protrudes into the outer medium. These cilia always have the regular 9X2+2 microtubule arrangement. Sensory cells terminate basally within the nerve plexus (e.g. Burke 1980, Ball & Jangoux 1990).

*Support cells*, the fourth cell category occurring in podial adhesive areas, are traversed by a bundle of filaments joining their apical and basal

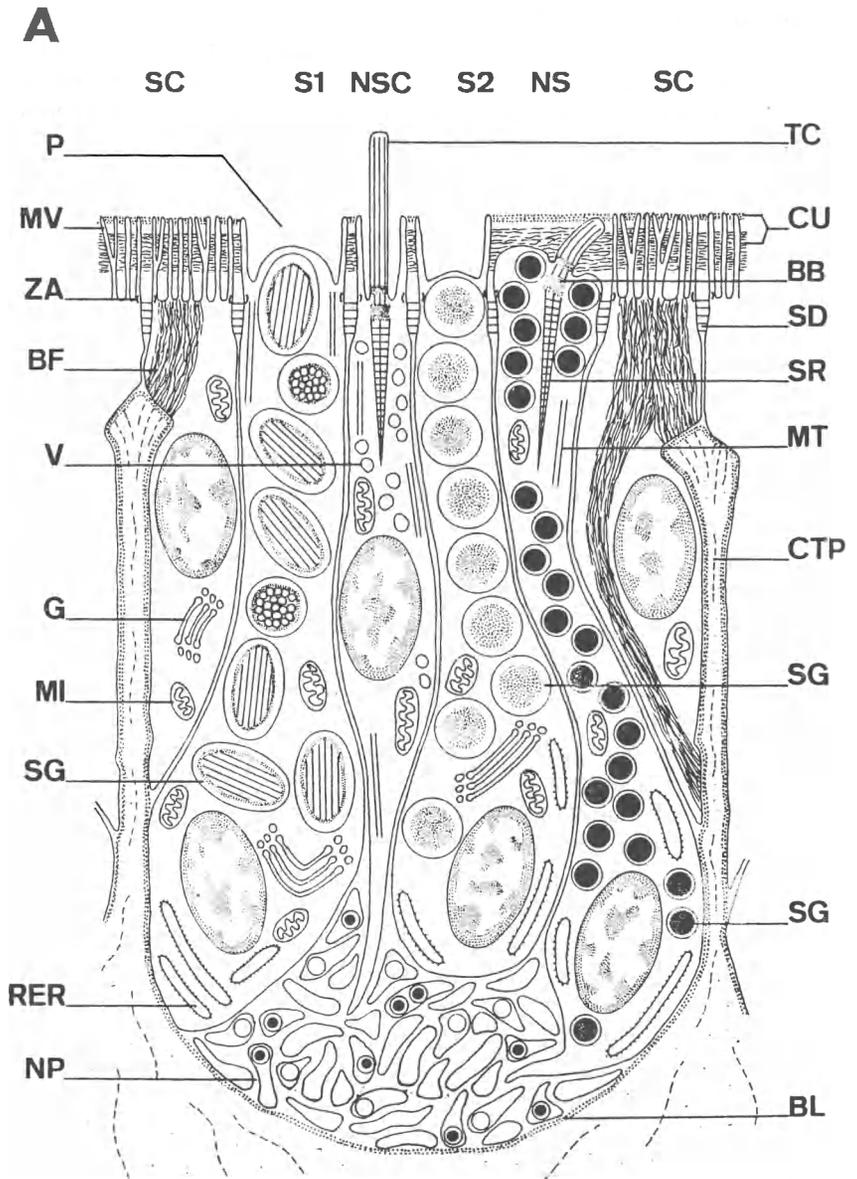


Figure 2. Reconstruction of epidermal adhesive areas of echinoderm podia (not to scale). A) Transverse section through a radial epidermal strip located between two adjacent connective tissue laminae of a podium of the asteroid *Asterias rubens* (from Flammang et al. 1994).

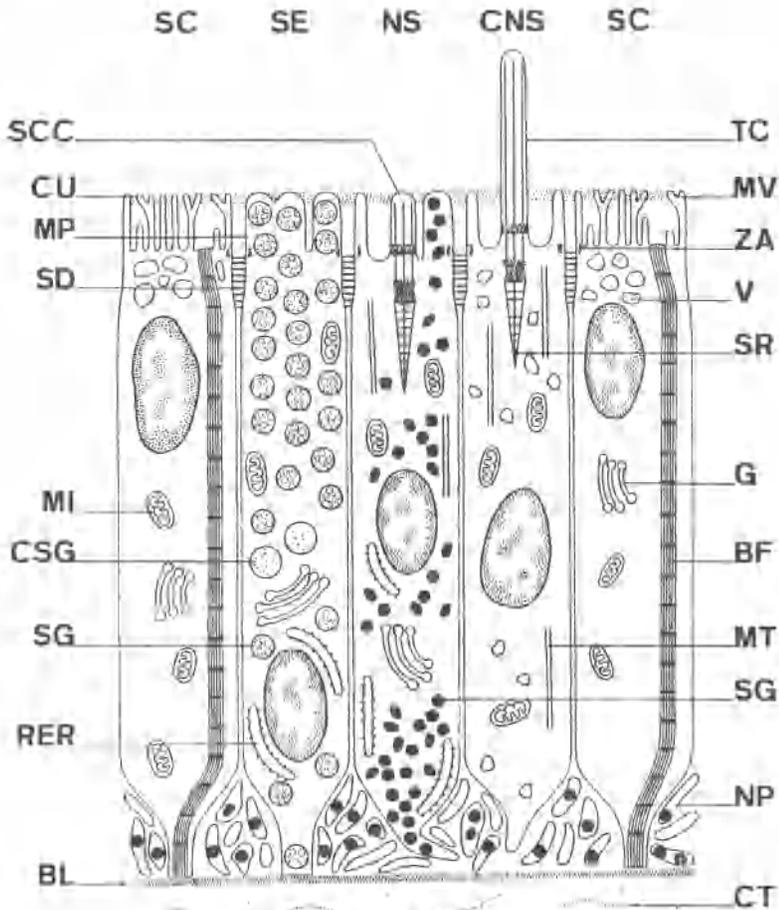
**B**

Figure 2. (Continued). B) Longitudinal section through the central disc epidermis of a peristomeal podium of the echinoid *Sphaerechinus granularis* (from Flammang & Jangoux 1993). BB = basal body, BF = bundle of filaments, BL = basal lamina, CNS = sensory cell, CSG = condensing secretory granule, CT = connective tissue, CTP = connective tissue protrusion, CU = cuticle, G = Golgi zone, MI = mitochondrion, MP = microvillar-like cell projection, MT = microtubule, MV = microvillus, NP = nerve plexus, NS = neurosecretory-like cell, NSC = sensory cell, P = pore, RER = rough endoplasmic reticulum cisternae, S1 = Type 1 secretory cell, S2 = Type 2 secretory cell, SC = support cell, SCC = subcuticular cilium, SD = septate desmosome, SE = secretory cell, SG = secretory granule, SR = striated rootlet, TC = transcuticular cilium, V = vesicle, ZA = zonula adhaerens.

Table 2. Comparison of the fine structure of podial adhesive systems in echinoderms.

Class	Order	Species	Podia ( <i>shape and function</i> )	Secretory cells ( <i>Name and description</i> )	Neurosecretory-like cells ( <i>Name and description</i> )	Sensory cells ( <i>Name and description</i> )	Cellular organization in the podial adhesive area	References
Echinoidea	Diadematoidea	<i>Diadema antillarum</i>	Coronal disk-ending podia Attachment	Secretory cells Dense-cored granules (400 nm)	Not described	Not described	Homogeneous secretory epidermis	Coleman 1969
	Echinoidea	<i>Strongylocentrotus droebachiensis</i> , <i>Lytechinus pictus</i> and <i>Lytechinus variegatus</i>	Coronal disk-ending podia Attachment	<b>Disk central area</b> <i>Type I collocytes</i> Heterogeneous granules (250 nm) <b>Disk peripheral area</b> <i>Type II collocytes</i> Homogeneous granules (250 nm)	Not described	<b>Disk central area</b> <i>Sensory cells</i> Transcuticular cilium	Homogeneous secretory epidermis	Burke 1980
		<i>Sphaerechinus granularis</i>	Coronal disk-ending podia Attachment	<i>NCS cells</i> Granules with a central fibrillar bundle (250-350 nm)	<i>CS cells</i> Dense-cored granules (150 × 250 nm)	<i>CNS cells</i> Transcuticular cilium (5µm)	Homogeneous secretory epidermis	Flammang & Jangoux 1993
			Peristomeal disk-ending podia Feeding	<i>NCS cells</i> Heterogeneous granules (250 nm)	<i>CS cells</i> Dense-cored granules (150 × 250 nm) Subcuticular cilium (4µm)	<i>CNS cells</i> Transcuticular cilium (5µm)	Homogeneous secretory epidermis	Flammang & Jangoux 1993

Table 2. (Continued).

Class	Order	Species	Podia ( <i>shape and function</i> )	Secretory cells ( <i>Name and description</i> )	Neurosecretory-like cells ( <i>Name and description</i> )	Sensory cells ( <i>Name and description</i> )	Cellular organization in the podial adhesive area	References
	Clype-asteroidea	<i>Laganum depressum</i>	<i>Accessory disk-ending podia</i> Feeding	<b>Disk central area</b> <i>S1 cells</i> Dense-cored granules (300 nm)  <b>Disk intermediate area</b> <i>S2 cells</i> Granules with a central fibrillar bundle (300 nm) <i>S4 cells</i> Homogeneous granules (1 × 0,8µm)	<b>Disk central area</b> <i>S3 cells</i> Dense-cored granules (75 nm)  <b>Disk intermediate area</b> <i>S3 cells</i> Dense-cored granules (75 nm)	<i>C1 cells</i> Transcuticular cilium (3,5µm) <i>C2 cells</i> Transcuticular cilium (5,5µm)	C1 and C2 sensory cells are arranged in two concentric circles delimiting the disk central and intermediate areas, respectively. The disk central area is made up of S1 secretory cells and S3 neurosecretory-like cells; the disk intermediate area of S2 and S4 secretory cells and S3 neurosecretory-like cells	Flammang & Jangoux 1994
	Spatangoida	<i>Echinocardium cordatum</i>	<i>Penicillate podia</i> Feeding or burrowing	<i>NCS cells</i> Heterogeneous granules (150-230 nm)	<i>CS cells</i> Dense-cored granules (70-100 nm) Subcuticular cilium (1,5µm)	<i>CNS cells</i> Transcuticular cilium (5 µm)	Epidermal complexes made up of 1 secretory cell, 1 neurosecretory-like cell and 2 sensory cells	Flammang et al. 1991
Asteroidea	Paxillosida	<i>Astropecten</i> sp.	<i>Knob-ending podia</i> Locomotion and burrowing	<i>Large-granule cells</i> Dense-cored granules (800 × 500 nm)	<i>Small-granule cells</i> Homogeneous granules (80-160 nm)	<i>Ciliated cells</i>	Not described	Engster & Brown 1972

Table 2. (Continued).

Class	Order	Species	Podia ( <i>shape and function</i> )	Secretory cells ( <i>Name and description</i> )	Neurosecretory-like cells ( <i>Name and description</i> )	Sensory cells ( <i>Name and description</i> )	Cellular organization in the podial adhesive area	References
		<i>Luidia ciliaris</i> and <i>Luidia maculata</i>	<i>Knob-ending podia</i> Locomotion and burrowing	<i>S1 cells</i> Granules with a central fibrillar bundle (1,5 × 1µm) <i>S2 cells</i> Dense-cored granules (1µm)	<i>Neurosecretory cells</i> Dense-cored granules (200-350 µm)	<i>Non-secretory ciliated cells</i> Transcuticular cilium (3µm)	Homogeneous secretory epidermis	Flammang 1995
		<i>Luidia penangensis</i>	<i>Knob-ending podia</i> Locomotion and burrowing	<i>S1 cells</i> Granules with a central fibrillar bundle (1,5 × 1µm)	<i>Neurosecretory cells</i> Dense-cored granules (200-350 nm)	<i>Non-secretory ciliated cells</i> Transcuticular cilium (3µm).	The sensory cells are gathered in islets surrounded by areas enclosing secretory and neurosecretory-like cells	Flammang 1995
	Valvatida	<i>Acanthaster planci</i> and <i>Patiria miniata</i>	<i>Disk-ending podia</i> Locomotion and attachment	Granules with a central fibrillar bundle (500-750 nm)	Not described	Not described	Homogeneous secretory epidermis	Harrison & Philpott 1966
		<i>Asterina stellifera</i>	<i>Disk-ending podia</i> Locomotion and attachment	<i>Type A secretory cells</i> Granules with a central fibrillar bundle (1,3-1,5µm)	Not described	Not described	Not described	Souza Santos & Silva Sasso 1968
	Forcipulatida	<i>Asterias forbesi</i>	<i>Disk-ending podia</i> Locomotion and attachment	<i>Type 1 secretory cells</i> Granules with a central fibrillar bundle (750 × 500 nm) <i>Type 2 secretory cells</i> Dense-cored granules (400-550 nm)	Not described	Not described	Homogeneous secretory epidermis	Chaet & Philpott 1964, Chaet 1965

Table 2. (Continued).

Class	Order	Species	Podia ( <i>shape and function</i> )	Secretory cells ( <i>Name and description</i> )	Neurosecretory-like cells ( <i>Name and description</i> )	Sensory cells ( <i>Name and description</i> )	Cellular organization in the podial adhesive area	References
		<i>Asterias forbesi</i> and <i>Pisaster giganteus</i>	<i>Disk-ending podia</i> Locomotion and attachment	Granules with a central fibrillar bundle (500-750 nm) (A 2nd secretory cell type can be distinguished on Fig.1. enclosing dense-core granules)	Not described	Not described	Homogeneous secretory epidermis	Harrison & Philpott 1966
		<i>Asterias rubens</i> and <i>Marthasterias glacialis</i>	<i>Disk-ending podia</i> Locomotion and attachment	<i>NCS1 cells</i> Granules with a central fibrillar bundle (1 × 0,6µm) <i>NCS2 cells</i> Dense-cored granules (500 nm)	<i>CS cells</i> Dense-cored granules (250-450 nm) Subcuticular cilium	<i>NSC cells</i> Transcuticular cilium (3µm)	Homogeneous secretory epidermis	Flammang et al. 1994
Holo-thuroidea	Dendrochirotida	<i>Neopentadactyla mixta</i>	<i>Ramified podia (tentacles)</i> Feeding	<i>Papillate cells</i> Dense-cored granules (300-500 nm)	<i>Granular cells</i> Homogeneous granules (130 nm)	<i>Ciliated cells</i> Transcuticular cilium (5µm)	Not described	T.B. Smith 1983
		<i>Ocnus brunneus</i> , <i>Ocnus lacteus</i> , <i>Thyone fusus</i> , <i>Thyone roscovita</i> , <i>Duasmiodactyla commune</i> and <i>Thyonidium pellucidum</i>	<i>Ramified podia (tentacles)</i> Feeding	<i>Type 1 papillar cells</i> Dense-cored granules (200-300 nm)	<i>Type 2 papillar cells</i> Homogeneous granules (60-100 nm)	<i>Ciliated cells</i> Transcuticular cilium	Epidermal complexes made up of 1 secretory cell and 1 neurosecretory-like cell	McKenzie 1987

Table 2. (Continued).

Class	Order	Species	Podia ( <i>shape</i> and <i>function</i> )	Secretory cells ( <i>Name</i> and <i>description</i> )	Neurosecretory-like cells ( <i>Name</i> and <i>description</i> )	Sensory cells ( <i>Name</i> and <i>description</i> )	Cellular organization in the podial adhesive area	References
		<i>Thyone briareus</i> and <i>Cucumaria rubra</i>	<i>Disk-ending podia</i> Locomotion and attachment	Capped granules (1µm)	Not described	Not described	Not described	Harrison 1968
	Aspidochirotida	<i>Parastichopus californicus</i>	<i>Ramified podia (tentacles)</i> Feeding	Dense-cored granules (0,6-0,7µm)	(A neurosecretory-like cell can be distinguished on Fig. 10.)	<i>Unciliated cells</i>	Not described	Cameron & Fankboner 1984
		<i>Holothuria forskali</i>	<i>Ramified podia (tentacles)</i> Feeding	<i>Glandular vesicular cells</i> Dense-cored granules (300-500 nm)	Not described	<i>Ciliated cells</i> Transcuticular cilium (10- 13µm)	Not described	Bouland et al. 1982
			<i>Disk-ending podia</i> Locomotion and attachment	<i>NCS1 cells</i> Apical tuft cells Dense-cored granules (250 nm) <i>NCS2 cells</i> Apical duct cells Capped granules (1 µm)	<i>CS cells</i> Homogeneous granules (150 µm) Subcuticular cilium (2,5 µm)	<i>CNS cells</i> Transcuticular cilium (4µm)	Homogeneous secretory epidermis	Flammang & Jangoux 1992a
		<i>Stichopus variegatus</i> , <i>Parastichopus californicus</i> and <i>Parastichopus parvimensis</i>	<i>Disk-ending podia</i> Locomotion and attachment	Capped granules (2 × 1 µm) (A 2nd secretory cell type can be distinguished on Figs 3 and 11); dense-cored granules (250 µm)	Not described	Not described	Not described	Harrison 1968
	Apodida	<i>Leptosynapta</i> sp.	<i>Ramified podia (tentacles)</i> Feeding	<i>Type 1 cells</i> Dense-cored granules (100-150 nm)	<i>Type 2 cells</i> Homogeneous granules (30-45 nm)	<i>Unciliated cells</i> Subcuticular cilium	Not described	McKenzie 1988a

Table 2. (Continued).

Class	Order	Species	Podia ( <i>shape and function</i> )	Secretory cells ( <i>Name and description</i> )	Neurosecretory-like cells ( <i>Name and description</i> )	Sensory cells ( <i>Name and description</i> )	Cellular organization in the podial adhesive area	References
Ophiuroidea	Phryno- phiurida	<i>Asteronyx loveni</i>	<i>Digitate podia</i> Handling (feeding?)	<i>NCS cells</i> Dense-cored granules (850 × 650 nm)	<i>CS cells</i> Homogeneous granules (75 nm) Subcuticular cilium	<i>CNS cells</i> Transcuticular cilium (3 μm)	Epidermal complexes made up of 2 secretory cells, 1 neurosecretory-like cell and 1 sensory cell	Flammang, unpubl. obs.
	Ophiurida	<i>Ophiocomina nigra</i>	<i>Knob-ending podia</i> Feeding	<i>Type A secretory cells</i> Dense-cored granules (700 × 450 nm)	<i>Neurosecretory-like cells</i> Dense-cored granules (100 nm) Subcuticular cilium	<i>Sensory cells</i> Transcuticular cilium (1,5 μm)	Epidermal complexes made up of 2 secretory cells, 1 neurosecretory-like cell and 1 sensory cell	Ball & Janguoux 1990
		<i>Hemipholis elongata</i>	<i>Digitate podia</i> Handling	<i>Mucus-secretory cells</i> Heterogeneous granules (400 nm)	(Neurosecretory-like cells can be distinguished on Figs 8 and 10)	<i>Ciliated cells</i> Transcuticular cilium	Epidermal complexes made up of 2 secretory cells, 1 neurosecretory-like cell and 1 sensory cell	Hajduk 1992
Crinoidea	Comatulida	<i>Comatula purpurea</i> , <i>Colobometra per-spinosa</i> , <i>Stephanometra oxycantha</i> , <i>Lamprometra palmata</i> and <i>Antedon bifida</i>	<i>Digitate podia</i> Feeding	<b>Papillae</b> <i>Type A secretory cells</i> Heterogeneous granules (700 nm) <i>Type C secretory cells</i> Heterogeneous granules (1 × 0,5 μm)	<b>Papillae</b> <i>Nerve cells</i> Dense-cored granules (100 nm) Transcuticular cilium	<b>Papillae</b> <i>Nerve cells</i> Dense-cored granules (100 nm) Transcuticular cilium	Epidermal complexes made up of type A and type C secretory cells and about 12 nerve cells	McKenzie 1992

Table 2. (Continued).

Class	Order	Species	Podia ( <i>shape</i> and function)	Secretory cells ( <i>Name</i> and description)	Neurosecretory-like cells ( <i>Name</i> and description)	Sensory cells ( <i>Name</i> and description)	Cellular organization in the podial adhesive area	References
		<i>Antedon bifida</i>	<i>Digitate podia</i> Feeding	<b>Papillae (on all podia)</b> <i>S1 cells</i> Dense-cored granules (1 µm) <i>S2 cells</i> Vacuoles <b>Hillocks (only on tertiary podia)</b> <i>S3 cells</i> Heterogeneous granules (400 nm) Transcuticular cilium (1 µm)	<b>Papillae (on all podia)</b> (Neurosecretory-like cells were never observed in papillae) <b>Hillocks (only on tertiary podia)</b> <i>S4 cells</i> Dense-cored granules (200 nm) Subcuticular cilium	<b>Papillae (on all podia)</b> <i>Neuroepithelial cells</i> Transcuticular cilium (2 µm) <b>Hillocks (only in tertiary podia)</b> <i>Neuroepithelial cells</i> Transcuticular cilium (2 µm)	Both papillae and hillocks are epidermal complexes. Papillae are made up of about 4 S1 secretory cells, 6 S2 secretory cells and 10 sensory cells. Hillocks are made up of 2 S3 secretory cells, 1 neurosecretory-like cell (S4 cell) and a few sensory cells.	Flammang & Jangoux 1992b

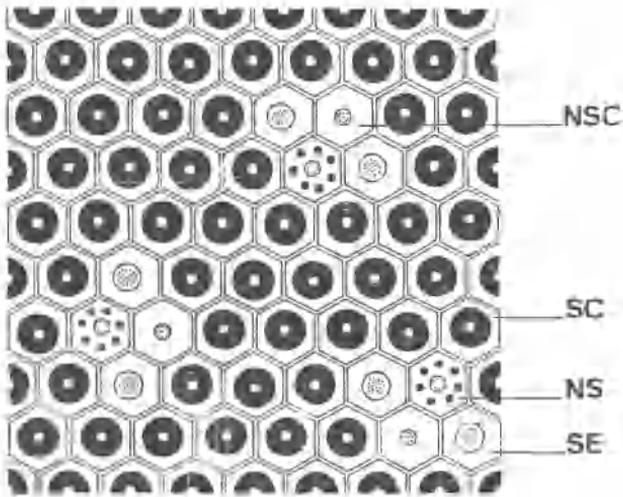
membranes (Fig. 2, Plates 3.7 and 3.8). According to Harris & Shaw (1984), this bundle is made up of intermediate filaments that may act as tension-bearing structures (Alberts et al. 1994). Support cells are particularly well-developed in the adhesive epidermis of locomotory podia where they are T-shaped (Fig. 2A). Almost all of their cytoplasm, i.e. that of both the cell body and its thin apico-lateral processes, is occupied by the bundle of filaments. In the lateral processes, these filaments are connected basally, via hemidesmosomes, to the collagen fibers of connective tissue protrusions. The latter arise from the underlying connective tissue layer and insinuate themselves between the epidermal cells to reinforce the adhesive area (Flammang & Jangoux 1992a, 1993, Flammang et al. 1994).

In crinoids, support cells from the podial adhesive areas (the so-called central cell of papillae and hillocks) are unique in that they contain a central bundle consisting of several hundred microtubules and not of intermediate filaments (Holland 1969, Flammang & Jangoux 1992b, McKenzie 1992).

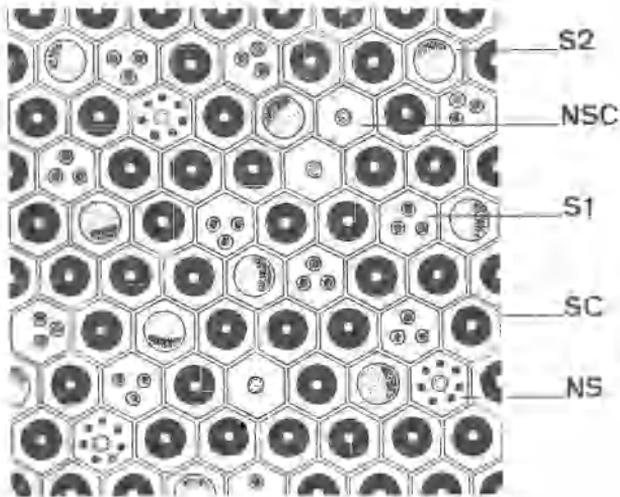
*Cuticle.* A cuticle, consisting of fibrous and sometimes granular material, covers the epidermal cells of echinoderm podial adhesive areas (Fig. 2, Plates 3.7 and 3.8) (Holland & Neilson 1978, McKenzie 1988c). This cuticle is traversed only by the tips of the cilia of the sensory cells, and, in species possessing apical duct secretory cells, is interrupted only by their secretory pores. The cuticle is separated from the epidermis by a subcuticular space that is crossed by the epidermal cell microvilli.

The cuticle is generally poorly preserved with the classical glutaraldehyde fixation, and special fixatives must be used to study its organization (Holland & Neilson 1978, McKenzie 1988c, Campbell & Crawford 1991). Depending on the species, there are from three to five cuticular sublayers. The most external, present in all species, is the 'fuzzy coat' and consists of numerous fibrils (McKenzie 1988c).

*Cellular organization* of the podial adhesive areas varies according to whether the podia are handling or locomotory though in both cases secretory, neurosecretory-like and sensory cells are always closely associated (Table 2, Fig. 3). In the epidermis of handling podia, these cells join together to form sensory-secretory complexes in which the three cell types are present (Fig. 3A). Such complexes occur, for example, in spat-angoid podia, in holothuroid tentacles, and in ophiuroid (Plate 3.3) and crinoid podia (crinoids are exceptions, since one of their two types of sensory-secretory complexes, the papillae, is devoid of neurosecretory-like cells). Conversely, in the epidermis of locomotory podia, these three cell types form an homogeneous cellular layer together with support cells (Fig. 3B),



**A**



**B**

Figure 3. Diagrammatic representation of transverse sections through adhesive areas of echinoderm podia showing the different organizations of epidermal cells (not to scale). A) *Asteronyx loveni* (Ophiuroidea) (original). B) *Holothuria forskali* (Holothuroidea) (from Flammang & Jangoux 1992a). NS = neurosecretory-like cell, NSC = sensory cell, S1 = Type 1 secretory cell, S2 = Type 2 secretory cell, SC = support cell, SE = secretory cell.

as is the case in regular echinoid, asteroid (Plate 3.1) and holothuroid podia. These cellular organizations suit the functions of the podia: a large adhesive area provides a strong attachment point during locomotion whereas discrete epidermal complexes are more efficient for the handling of small particles. A third and uncommon cellular organization occurs in the podia of the clypeasteroid echinoid *Laganum depressum* and in the podia of the paxillosid asteroid *Luidia penangensis*, in which the sensory cells are clustered and separated from the secretory areas (see Flammang & Jangoux 1994, Flammang 1995, respectively). Interestingly, these two species live in particulate substrata.

2.3.1.2 *A model for the adhesive mechanism.* Adhesion is the joining together of two dissimilar materials, the adherends, with a sticky material, the adhesive. The surface properties of the adherends and the chemical and physical properties of the adhesive determine the strength of adhesion (Waite 1983a). In echinoderm podial adhesion, the adherends are the epidermal cuticle on one side and a solid substratum (sea-bottom or particle) on the other; or more exactly, the fuzzy coat (the most external layer of the cuticle) and the primary film covering the substratum (the primary film is a thin layer, consisting of adsorbed macromolecules and bacteria, that coats all marine surfaces; Characklis 1981). The adhesive is present as a thin film between the cuticle and the substratum.

In view of the ultrastructure of the adhesive areas of echinoderm podia, it can be hypothesized that their epidermal cells are involved in adhesion and deadhesion and function as a duo-gland adhesive system as proposed by Hermans (1983). In the functional model proposed by Flammang et al. (1991), adhesive and de-adhesive secretions are produced by secretory and neurosecretory-like cells, respectively. This functional model of adhesion/de-adhesion matches well with the activities and behaviour of both locomotory and handling podia (see e.g. Flammang et al. 1991, Flammang & Jangoux 1993).

Secretory cells are considered to be adhesive on the basis of observations made on locomotory podia that were amputated and fixed while firmly attached to a substratum (attached podia). In these podia, the secretory cells have always released some of their secretory granules (Plates 4.2 and 4.3) (Flammang & Jangoux 1992a, Flammang et al. 1994). Moreover, they are the only cells having extruded secretory granules, the neurosecretory-like cells apparently have not released any granules (Flammang et al. 1994). In fact, secretory cells have been considered to be adhesive in every podium studied. The different ultrastructure of the granules of secretory cells in the different echinoderm taxa probably depends on the nature of their contents that, in turn, could be

related to the possible adhesive strength of the different podia (Engster & Brown 1972, Flammang & Jangoux 1993, Flammang 1995).

The adhesive material from secretory cells forms the adhesive layer joining the podium to the substratum (Plate 4.2) and remains on the substratum as a podial print after the podium has become detached (Thomas & Hermans 1985, Mooi 1986a, Flammang & Jangoux 1992a, 1993, Flammang et al. 1994). In the asteroids *Asterias rubens* and *Marthasterias glacialis*, the material of the adhesive layer is a compact fibrillar matrix about 5  $\mu\text{m}$  thick (Flammang et al. 1994).

De-adhesion could be due to the material enclosed in the granules of neurosecretory-like cells. Indeed, there must be a controlled detachment mechanism that allows locomotory podia to become detached easily from the substratum and allows handling podia to get rid of adhering particles. The neurosecretory-like cells are the most likely candidates for this function. Indeed, in podia that were cut off and fixed just after they voluntarily became detached from a substratum (detached podia), these cells appear to have released their most apical secretory granules (Plate 4.4) (Flammang, unpubl. obs.). McKenzie (1987) and Ball & Jangoux (1990) proposed that the granule contents of neurosecretory-like cells could act as a neurotransmitter terminating the release of adhesive material by the secretory cells. On the contrary, Flammang & Jangoux (1993) suggested that neurosecretory-like cell granules are released on the adhesive surface of the podia where their contents would act as a deadhesive. The breakage of the adhesive bond occurs between the surface of the podium and the adhesive material, the latter remaining strongly attached to the substratum and forming a podial print. It is possible that the deadhesive material and/or the fuzzy coat are incorporated in the podial prints (in TEM pictures of detached podia of *Asterias rubens*, the fuzzy coat can no longer be distinguished; Plate 4.4; Flammang, unpubl. obs.).

Sensory cells are closely associated with both secretory and neurosecretory-like cells in podial adhesive areas. These sensory cells, which have always been considered to be sensory in function (e.g. Engster & Brown 1972, Burke 1980, Bouland et al. 1982, Ball & Jangoux 1990, Flammang & Jangoux 1992b), are the first to contact the substratum with their transcuticular cilium. Consequently, their stimulation could trigger the release of adhesive material by the secretory cells via the nerve plexus. Most authors agree that neurosecretory-like cells are sensory too (T.B. Smith 1983, McKenzie 1987, Ball & Jangoux 1990, Flammang et al. 1991). It is possible that the stimulation of their subcuticular cilium is necessary to induce the release of their secretory granules.

In the podial epidermis of several echinoderm species, the adhesive areas enclose two types of secretory cells (Fig. 2A, Plates 3.1 and 3.5; see also Table 2). In the locomotory disc-ending podia of asteroids and

holothuroids, it was proposed that one type of adhesive cell is used only in locomotion on horizontal substrata, whereas both types are necessary during locomotion on vertical substrata or for attachment, when a stronger adhesive bond is required (McKenzie 1988b, Flammang et al. 1994). However, this hypothesis can hardly apply to the locomotory knob-ending podia of the paxilloid asteroids *Luidia ciliaris* and *Luidia maculata* that dwell on particulate substrata (Flammang 1995), and even less to the handling podia of comatulid crinoids and clypeasteroid echinoids (Flammang & Jangoux 1992b, 1994; respectively). In these species, the two secretions may combine to form a special type of adhesive secretion. However, the significance of two types of adhesive cells in the adhesive areas of echinoderm podia remains obscure.

The podia of crinoids, the most primitive of the extant echinoderm classes, are an obvious place to look for indications of an ancestral adhesive system. *Antedon bifida* possesses two adhesive systems: the papillae and the hillocks, both sensory-secretory complexes (Flammang & Jangoux 1992b). The papillae enclose two types of secretory cells supposed to be adhesive, but no neurosecretory-like cells. This seems to be a unique system in echinoderms. The hillocks, on the other hand, enclose secretory cells of a single type, i.e. adhesive cells, and one neurosecretory-like cell, i.e. a de-adhesive cell. This is a duo-glandular system equivalent to those occurring in the podia of other echinoderms. Therefore, of the two adhesive systems occurring in crinoid podia, one (the papilla-like system) appears to be restricted to crinoids while the other (the hillock-like system) is widespread throughout the phylum.

*2.3.1.3 Composition of the substances involved in the adhesive process.* In echinoderms, biochemical studies on the composition of the substances involved in the adhesive process are currently lacking but a theoretical molecular model has been proposed (Hermans 1983). In this model, the adhesive cells secrete basic proteins which, via their lysine and/or arginine residues, make electrostatic bonds between the acid mucopolysaccharides of the fuzzy coat (outer layer of the podial cuticle) and those of the primary film. The detachment is due to the release of acid mucopolysaccharides by the deadhesive cells. These acid mucopolysaccharides compete with the anionic sites on the cuticle for the basic residues of the adhesive proteins, thus the podia become detached.

However, Hermans' predictions, as far as the nature of the involved substances, have not been corroborated. This mostly comes from the results of histochemical tests performed on the podial epidermal adhesive areas. Indeed, the secretory cells (adhesive cells), in most species the most prominent cells of the adhesive areas, stain with dyes specific for acid mucopolysaccharides (Table 3). However, in some species, the his-

Table 3. Comparison of the composition of secretory cell (adhesive cell) granules in podial adhesive systems of echinoderms, using histochemistry.

Class	Order	Species	Secretory cell granule contents		References
			Proteins	Mucopolysaccharides	
Echinoidea	Cidaroida	<i>Cidaris cidaris</i>	-	+	Nichols 1961
	Diadematoidea	<i>Diadema antillarum</i>	-	+	Coleman 1969
	Echinoida	<i>Echinus esculentus</i>	-	+	Nichols 1961
		<i>Sphaerechinus granularis</i>	-	+	Defretin 1952, Flammang & Jangoux 1993
	Clypeasteroidea	<i>Echinocyamus pusillus</i>	-	+	Nichols 1959b
		<i>Echinarachnius parma</i>	+	-	Mooi 1986a
	Spatangoida	<i>Echinocardium cordatum</i>	-	+	Nichols 1959a, Flammang et al. 1991
Asteroidea	Paxillosida	<i>Astropecten</i> sp.	-	+	Engster & Brown 1972
		<i>Astropecten irregularis</i>	-	+	Defretin 1952
	Valvatida	<i>Asterina stellifera</i>	-	+	Souza Santos & Silva Sasso 1968
		Forcipulatida	<i>Asterias forbesi</i> (type 1 secretory cells)	-	+
	<i>Asterias rubens</i>		+	+	Perpeet & Jangoux 1973
	<i>Asterias rubens</i> and <i>Marthasterias glacialis</i>	-	+	Defretin 1952, Flammang et al. 1994	
Holothuroidea	Dendrochirotida	<i>Ocnus brunneus</i> , <i>Ocnus lacteus</i> , <i>Thyone fusus</i> , <i>Thyone roscovita</i> , <i>Duasmodactyla commune</i> and <i>Thyonidium pellucidum</i> (tentacles)	+	-	McKenzie 1987
		Aspidochirotida	<i>Parastichopus californicus</i> (tentacles)	-	+
	<i>Holothuria forskali</i> (tentacles)		+	+	Bouland et al. 1982

Table 3. (Continued).

Class	Order	Species	Secretory cell granule contents		References
			Proteins	Mucopolysaccharides	
		<i>Holothuria forskali</i> (podia)	-	+	Flammang & Jangoux 1992a
Ophiuroidea	Ophiurida	<i>Ophiocomina nigra</i>	+	-	Ball & Jangoux 1990
Crinoidea	Comatulida	<i>Antedon bifida</i>	-	+	Nichols 1960, Flammang & Jangoux 1992b

+ = detected; - = not detected.

tochemical tests indicate the presence of both acid mucopolysaccharides and proteins in the granules of secretory cells. In dendrochirote holothuroid tentacles and ophiuroid podia, only proteins have been demonstrated (Table 3). These differences in the composition of the adhesive material could be related to the function of the different podia. Indeed, locomotion, attachment, feeding or burrowing require different adhesive strengths and, therefore, adhesive secretions with different compositions. The neurosecretory-like cells (deadhesive cells) do not stain with any of the classical histochemical dyes and do not contain acid mucopolysaccharides.

At the ultrastructural level, Harrison & Philpott (1966) and Harrison (1968), using colloidal thorium, demonstrated that the acid mucopolysaccharides are not distributed homogeneously in the granules of secretory cells. In asteroid podia they form the outer rim in granules with a central filamentous bundle and they constitute the large electron-lucent part in the capped granules of holothuroid podia. These authors suggested that the material that is not labelled with colloidal thorium is probably protein. Similar results have been found in the podia of *Asterias rubens* where cationic colloidal gold labels anionic sites on the outer rim in granules with a central filamentous bundle of Type 1 secretory cells as well as in dense-cored granules of Type 2 secretory cells (Flammang, unpubl. obs.). Cationic colloidal gold also binds heavily to the cuticle's fuzzy coat.

The chemical composition of podial prints has been investigated. Using various dyes, it was demonstrated that the podial prints of *Sphaerechinus granularis* contain acid mucopolysaccharides but no proteins (Flammang & Jangoux 1993). Those of *Asterias forbesi* include proteins (Chaet 1965) and the prints of both *Asterias rubens* and *Marthasterias glacialis* stain strongly for acid mucopolysaccharides and weakly for proteins (Flammang et al. 1994), as do the podial prints of *Holothuria forskali* (Flammang & Jangoux 1992a). The interpretation of these observations must take into account the fact that, in addition to adhesive material, podial prints likely contain deadhesive material or even cuticular material. On the other hand, Thomas & Hermans (1985) showed that podial prints of the asteroid *Leptasterias hexactis* were removed by trypsin, indicating the importance of their proteinic fraction in the adhesive interaction with the substratum. The podial prints of *Asterias rubens* have similar characteristics (Flammang, unpubl. obs.).

The chemical evidence is too weak to propose a molecular model for adhesion in echinoderms. However, it seems that the adhesive material is a protein-polysaccharide complex whose composition varies from one taxon to another. This material links the negatively charged fuzzy coat of the cuticle to the negatively charged primary film, presumably through

electrostatic interactions. These interactions could be direct, as proposed by Hermans (1983), or could require the presence of divalent cations in species in which acid mucopolysaccharides are the predominant part of the adhesive material. The composition of the deadhesive secretion remains unknown. It is possible that the deadhesive material interferes with the electrostatic bonds between the adhesive layer and the fuzzy coat (Hermans 1983). Another possibility is that it releases the fuzzy coat from the underlying cuticular layers. In this second hypothesis, the deadhesive material would act as an enzyme. Interestingly, some authors have suggested that podial secretions may include enzymes (Péquignat 1966, 1972, Chia 1969).

### 2.3.2 *Mechanical attachment*

It seems that disc-ending podia differ from other types of podia in that they use mechanical attachment in addition to the duo-glandular chemical attachment, their disc operating like a sucker (J.E. Smith 1937, 1947, Nichols 1959b, 1961, Mooi 1986a). The ability to use disc-ending podia in suction could have evolved independently in three echinoderm classes: asteroids, echinoids (both regular and irregular clypeasteroids), and holothuroids (Nichols 1962).

**2.3.2.1 *Structure and functioning of the disc.*** Compared with the basic structure of a podium wall (see Section 2.2.1), a typical disc shows the development of support structures (connective tissue) and the differentiation of particular muscular systems (Fig. 4).

At the distal end of a podium, at the level of the disc, lies a circular plate of connective tissue, the terminal plate, that is continuous on its proximal side with the connective tissue sheath of the stem. In holothuroids, this plate has a uniform thickness (Flammang & Jangoux 1992a). In echinoids and asteroids, its center, the diaphragm, is very much thinner than its margin which consists of a thick ring (J.E. Smith 1947, Nichols 1961). In the three classes, numerous arborescent connective tissue septa radiate from the distal surface of the terminal plate. The thinnest, distal branches of these septa insinuate themselves between the epidermal cells and attach apically to the support cells of the epidermis (J.E. Smith 1937, 1947, Nichols 1961, Flammang & Jangoux 1992a, 1993, Flammang et al. 1994)

In holothuroids and echinoids, the terminal plate encloses a calcified skeleton. In holothuroids, this skeleton consists of a large circular ossicle underlying the whole disc, surrounded by a ring of small elongated spicules (Nichols 1966, Flammang & Jangoux 1992a). In regular echinoids, the disc skeleton lies in the external part of the terminal plate and is made up of two superposed structures: a distal 'rosette' and a proximal 'frame'.

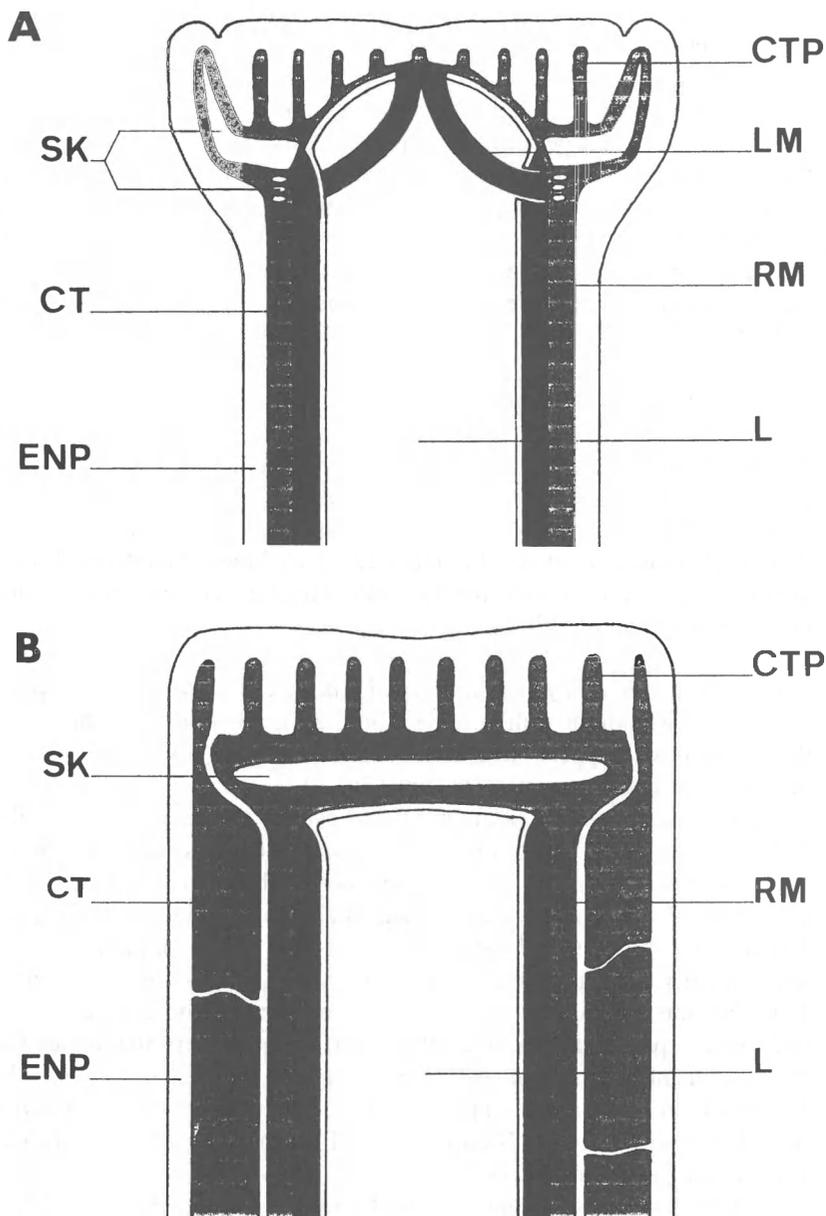


Figure 4. Schematic representation of longitudinal sections through the disc of echinoderm podia (original, not to scale). A) *Sphaerechinus granularis* (Echinoidea). B) *Holothuria forskali* (Holothuroidea). CT = connective tissue sheath, CTP = connective tissue protrusion, ENP = epidermis and nerve plexus, L = ambulacral lumen, LM = levator muscle, RM = retractor muscle, SK = skeleton.

The rosette is made up of four or five large ossicles, the frame consists of numerous small spicules. Both structures are ring-shaped and their center is occupied by the ambulacral lumen (Nichols 1961, Flammang & Jangoux 1993). In clypeasteroid echinoids, the disc skeleton, when present, is reduced to either a ring-shaped ossicle or a pair of symmetrical spicules, both surrounding the ambulacral lumen (Mooi 1986b).

As far as the disc musculature is concerned, different muscle systems can be distinguished in different classes. In addition to the retractor muscle common to all types of podia, disc-ending podia always possess a levator muscle that is arranged longitudinally and attaches distally to the center of the diaphragm (Smith 1947, Nichols 1959b, 1961, Mooi 1986a). Holothuroid disc-ending podia are exceptions since they lack this levator muscle, the retractor muscle being their only muscle system (Flammang & Jangoux 1992a). Other muscle systems have been described in disc-ending podia and proposed to be involved in sucker functioning, but their existence has been questioned. In the asteroid *Asterias rubens*, J.E. Smith (1947) described a muscle system made up of radial fibers attaching to the center of the diaphragm on one side and to the internal edge of the thickened, external part of the terminal plate on the other side. However, Perpeet & Jangoux (1973) concluded that these fibers are, in fact, the distal extremities of the fibers of both the retractor and the levator muscles. Disc-ending podia of clypeasteroid echinoids were described as possessing muscle fibers within their disc epidermis. These disc muscle fibers were supposed to attach to the distal surface of the terminal plate on one side and to the disc cuticle on the other side (Nichols 1959b, Mooi 1986). These muscle fibers are in fact the support cells of the epidermis. The staining affinities of their intracytoplasmic intermediate filaments, identical to those of myofilaments, have led authors to misinterpret support cells as intraepidermal muscle cells (Flammang & Jangoux 1994).

In all cases, when a disc-ending podium attaches to a substratum, the sucker effect is the consequence of the contraction of the levator muscle which lifts the diaphragm, thus creating a suction cavity (J.E. Smith 1947, Nichols 1959b, 1961, Mooi 1986a). The thickened, external part of the terminal plate maintains the shape of the disc and prevents the suction cavity from collapsing (J.E. Smith 1947). The way the sucker effect is suppressed, on the other hand, is less obvious. J.E. Smith (1947) proposed that detachment in asteroids is brought about by the contraction of radial muscle fibers that raise the pressure in the suction cavity. Nichols (1959b) and Mooi (1986a) suggested that detachment in clypeasteroid echinoids is due to the simultaneous contraction of disc muscle fibers and relaxation of levator muscle, which would lift the disc margin from the substratum. Both radial muscle fibers of asteroids and disc muscle fibers

of clypeasteroids were demonstrated to be misinterpretations of other structures. A common method of detachment could occur in all disc-ending podia through a peeling effect. The simultaneous relaxation of the levator muscle and asymmetrical contraction of the retractor muscle would lower the diaphragm as well as lift one side of the disc margin, thus suppressing the sucker effect. This is the model of detachment originally proposed by Nichols (1961) for regular echinoid disc-ending podia.

*2.3.2.2 Importance of suction in disc-ending podium attachment.* Early authors described disc-ending podia of holothuroids as suckered podia although the operation of the sucker has never been adequately explained (Nichols 1966). In fact, these podia do not end in a sucker, because the disc morphology (the occurrence of a large circular ossicle underlying the whole disc, the peripheral insertion of the retractor muscle, and the lack of a levator muscle) does not allow a mechanical sucker-like operation as described in the previous section. The adhesion of disc-ending podia of holothuroids to the substratum thus appears to rely entirely on the disc epidermal secretions (Nichols 1966, Flammang & Jangoux 1992a).

On the other hand, suction has often been regarded as the primary means of attachment in asteroid and echinoid disc-ending podia. Paine (1926), who studied the podia of the asteroid *Asterias vulgaris*, concluded that 56% of podial attachment is contributed by suction, and the rest by adhesive secretions. However, Thomas & Hermans (1985) found that podia of the seastar *Leptasterias hexactis* adhered very strongly to a fine-meshed, stainless steel plankton screen that precluded the podia from using suction. They questioned the methodology of Paine (1926). First, she measured total attachment by allowing podia to attach to glass and measured chemical attachment by allowing them to attach to the open ends of rubber tubes. Thomas & Hermans (1985) demonstrated that podia do not attach equally well to all substrata. Second, she assumed that only the periphery of a disc uses secretions for adhesion, since this adhesion was measured by allowing podia to attach to the open ends of tubing. The hollow center of tubing not only prevented suction from forming, but also eliminated an unknown proportion of chemical attachment. Thomas & Hermans (1985) thus concluded that, although asteroid podia may use suction, it is a secondary adjunct to the adhesion established by secretions.

Morphological data from echinoid and asteroid podia support this hypothesis (Flammang & Jangoux 1993, Flammang et al. 1994). First, numerous epidermal secretory cells cover the entire apical surface of the disc. Second, the podial prints are completely (or almost completely) full of adhesive material. Third, podia may adhere strongly with only the

margin of their disc, leaving crescent-shaped podial prints. These complementary features argue for an adhesive process mediated principally by secretion. In this event, the levator muscle would flatten the apical surface of the disc for, in protracted podia, the central part of the disc forms a conical projection due to the increased internal hydrostatic pressure exerted by the ambulacral fluid (Flammang & Jangoux 1993). This flattening would allow all secretory cells to make contact with the substratum and to release their adhesive material. However, suction cannot be ruled out altogether. The levator muscle in the podial disc can probably also develop suction sufficient to reinforce adhesion.

### 2.3.3 *Strength of attachment*

The adhesive forces produced by echinoderm podia have been measured in a few cases. For practical considerations, these measurements have always involved locomotory, disc-ending podia. The total pull of all podia together has been measured in several asteroid species. Feder (1955) measured up to 4 kg (39.64 N) in *Pisaster ochraceus*, Lavoie (1956) over 3 kg (29.43 N) in *Asterias forbesi*, and Christensen (1957) 5 kg (49.05 N) in *Evasterias troscheli*. Total adhesive forces have also been measured in echinoids (Yamasaki et al. 1993). They range from 0.2 to 2.4 kg (1.96–23.54 N) in *Strongylocentrotus nudus*, and from 0.3 to 2.8 kg (2.94–27.47 N) in *Strongylocentrotus intermedius*. Unfortunately, the results from asteroids and echinoids cannot be compared because of differences in the experimental setup. Moreover, the substrata employed were different, Bivalve shells for asteroids (Feder 1955, Lavoie 1956) and smooth glass for echinoids (Yamasaki et al. 1993). Podia do not attach equally well to all substrata (Thomas & Hermans 1985). Adhesive forces depend on the mechanical and chemical properties of the substrata (Baier et al. 1968, Maroudas 1973, 1975).

Tenacity of single podia has been investigated (Paine 1926). She calculated that the average adhesive force of each podium of the asteroid *Asterias vulgaris* is 29.4 g (0.29 N), i.e. 17.7 g/mm<sup>2</sup> ( $1.7 \times 10^5$  N/m<sup>2</sup>), assuming that the tension exerted on an attached podium at the time of release is the maximum tension sustainable. However, this is probably not the case. Indeed, this ignores the 'free will' aspect of podial release, i.e. attachment to surfaces does not appear to be governed by one simple reflex but depends partly upon the 'willingness' of the animal (Thomas & Hermans 1985). This response explains the large range of results Paine (1926) reported. Moreover, when well-attached asteroids are pulled from substrata the stems of many podia break, leaving the discs and portions of stems attached to the substrata. Obviously, the ability of a disc to adhere exceeds the tensile strength of the stem. Therefore, the maximum adhe-

sive force podia can produce could be greater than the value calculated by Paine (1926).

### 3 OTHER ATTACHMENT MECHANISMS OF ECHINODERMS

In addition to podial adhesion, shared by all echinoderms, some groups possess other attachment mechanisms peculiar to them. Among them are mechanical and chemical attachments.

Mechanical attachments are less numerous and are usually found in crinoids. Some stalked bourgueticrinids anchor in soft substrata by branched roots which may have a terminal plate (Breimer 1978). Most crinoids (both comatulid and isocrinid) attach to the substratum with their cirri which are used as hooks to grasp (Breimer 1978, Lawrence 1987). Some comatulids that have no or weakly developed cirri attach by the arms and pinnules. In these species, the distal pinnules bear recurved hooks (grapnels) and are used as tethers to assist in maintaining position (Lawrence 1987). Attachment by the arms also occur in euryalid ophiuroids which have the ability to coil their arms around objects such as coral branches (Lawrence 1987).

Chemical attachments may be involved in a variety of functions such as fixation to the substratum, attachment of eggs and larvae, or defence. Some of these chemical attachments are relatively little-known such as the adhesion of the basal attachment disc of millericrinid, cyrtocrinid and bourgueticrinid crinoids to hard substrata (Breimer 1978, Lawrence 1987), or the adhesion of the eggs and embryos of some comatulid crinoids to their genital pinnules (Lahaye & Jangoux 1989, Heinzeller & Welsch 1994). The adhesive structures involved in these processes have not been studied in detail. Other adhesive structures were studied either because they are widely distributed throughout the phylum or because they are conspicuous. These are the larval and postlarval adhesive structures and the holothuroid Cuvierian tubules.

#### 3.1 *Larval and postlarval adhesive structures*

In most echinoderms, settlement and metamorphosis transform a bilaterally symmetrical and pelagic larva into a radially symmetrical and benthic postmetamorphic individual. Some echinoderm larvae settle first and then metamorphose; others metamorphose first and then settle (Strathmann 1978). In both cases, adhesive structures attach either the larva or the postlarva to the substratum during settlement. In three of the five extant echinoderm classes, these structures are the podia of the metamorphic or postmetamorphic stage, viz. the five primary podia of

competent echinoplutei in echinoids, the five primary tentacles (and, in some species, two posterior podia) of pentactulae in holothuroids, the five primary podia and the five first pairs of podia of ophiuroid postlarvae (Dawydoff 1948, Strathmann 1978). These podia seem to be similar in structure to adult podia (Burke 1980, Cameron & Fankboner 1984). Crinoids and asteroids possess larval adhesive structures that have no equivalent in the postmetamorphic stage (with the exception of paxilloid asteroids which lack these structures and attach by the podia of the postlarvae) (Strathmann 1978).

### 3.1.1 Crinoidea

The understanding of development in crinoids is derived entirely from studies on comatulids. These animals have the most complicated life-cycle within the Echinodermata, with no fewer than five successive stages: the embryo, the doliolaria stage (free swimming stage), the cystidean and the pentacrinoid stages (attached stages) and the adult stage. Metamorphosis lasts from the fixation of the doliolaria to the appearance of the pentacrinoid and includes the whole cystidean stage which is thus the metamorphic stage (Mladenov & Chia 1983, Lahaye & Jangoux 1987).

Competent doliolariae are small barrel-shaped larvae. They possess an attachment complex at their anterior end which consists of a ciliary cap surrounding a central core characterized by an apical tuft of elongated cilia and a ventrally located and slightly depressed adhesive pit (Fig. 5).

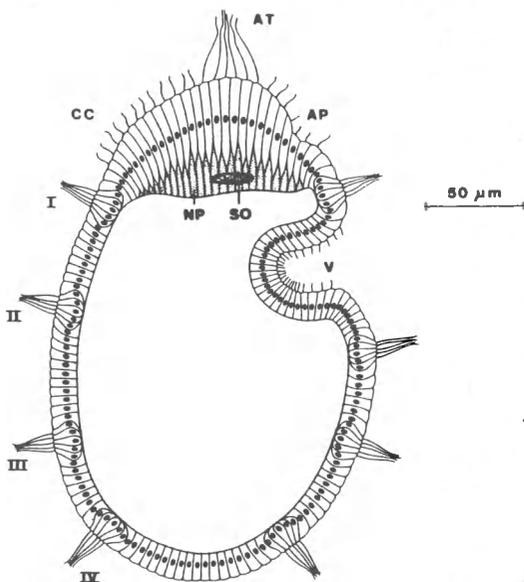


Figure 5. Diagram of a competent doliolaria larva of the comatulid crinoid *Antedon bifida* (from Jangoux & Lahaye 1990). AP = adhesive pit, AT = apical tuft, CC = ciliary cap, NP = nerve plexus, SO = subapical sensory structure, V = vestibule, I-IV = ciliary bands.

The ultrastructure of the attachment complex has been studied in the comatulids *Florometra serratissima* and *Antedon bifida* (Chia et al. 1986, Jangoux & Lahaye 1990, respectively). The attachment complex of doliolariae is strictly epidermal and is made up of elongated ciliated cells associated with a thick basiepidermal nerve plexus. The four types of cells forming the complex are ciliated non-secretory cells of two different types (A and B), and ciliated secretory cells of two different types (C and D) (Fig. 6). Type A ciliated non-secretory cells occur all over the attachment complex. They are the only cell type constituting the central core, their long cilia forming the apical tuft. These cells are thought to be sensory in function. Type B ciliated non-secretory cells occur exclusively in the ciliary cap. They each bear a long vibratile cilium which is however shorter than the one of Type A ciliated non-secretory cells. Type C ciliated secretory cells are distributed all over the ciliary cap but appear to be more numerous toward the rim of the adhesive pit in which a few of them also occur. These cells possess a long cilium. Much of their cytoplasm is filled with membrane-bound secretory granules (up to 2  $\mu\text{m}$  in diameter) which contain a flocculent material. These granules were shown histochemically to contain acid mucopolysaccharides. Type D ciliated secretory cells are restricted to the adhesive pit where they are the most abundant cell type. Each is provided with a short cilium. These cells are filled with membrane-bound secretory granules (up to 4  $\mu\text{m}$  in diameter) with an electron dense fibrillar proteinaceous contents.

Comatulid doliolariae attach to the substratum before they undergo metamorphosis. Larval adhesion may be transitory or permanent, depending presumably on the quality of the substratum (Mladenov & Chia 1983, Lahaye & Jangoux 1988). At the beginning of the settlement phase, the doliolaria becomes demersal and brushes the substratum with its apical tuft (sensory structure) (Mladenov & Chia 1983, Lahaye & Jangoux 1988). This implies the occurrence of a mechanism allowing the larva to combine loose adhesion to the substratum and movement. This might be the function of the Type C ciliated secretory cells of the ciliary cap whose secretions would produce a thin mucous film that would retain the larva at the water-substratum interface (Jangoux & Lahaye 1990). When meeting a favourable site, the larva stops moving and turns round on itself with its body directed obliquely (the adhesive pit facing the substratum) (Mladenov & Chia 1983, Lahaye & Jangoux 1988). If the substratum is not appropriate, the larva detaches and reinitiates the whole process. If the substratum is appropriate, the doliolaria becomes permanently fixed and transforms into a cystidean larva. Permanent adhesion occurs when Type D ciliated secretory cells secrete their proteinaceous cement (Chia et al. 1986, Jangoux & Lahaye 1990).

Both the cystidean and the pentacrinoid stages are attached to the sub-

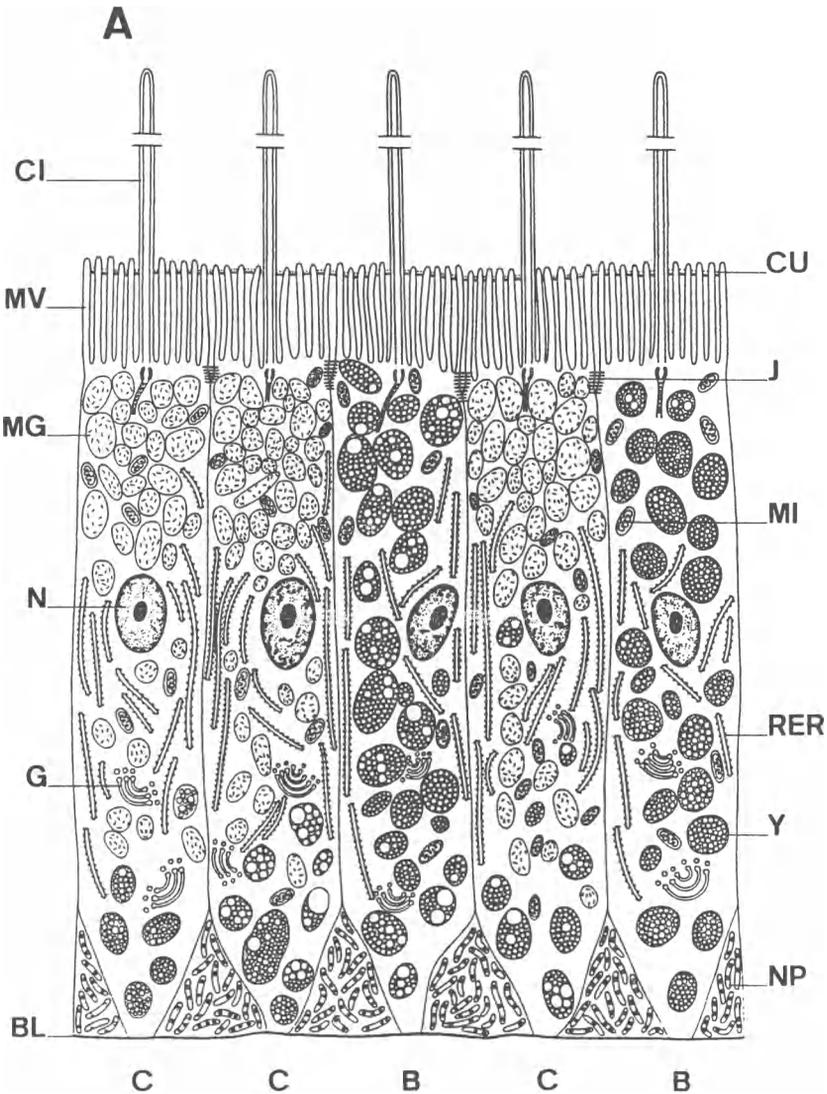


Figure 6. Diagrammatic representation of the cells of the ciliary cap (A) and of the adhesive pit (B) of the attachment complex in the doliolaria larva of the comatulid crinoid *Antedon bifida* (modified from Jangoux & Lahaye 1990). A = Type A ciliated non-secretory cell, B = Type B ciliated non secretory cell, BL = basal lamina, C = Type C ciliated secretory cell, CI = cilium, CU = cuticle, D = Type D ciliated secretory cell, G = Golgi complex, J = septate junction, MG = mucous secretory granule, MI = mitochondria, MV = microvilli, N = nucleus, NP = nerve plexus, PG = proteinic secretory granule, RER = rough endoplasmic reticulum, Y = yolk granule.

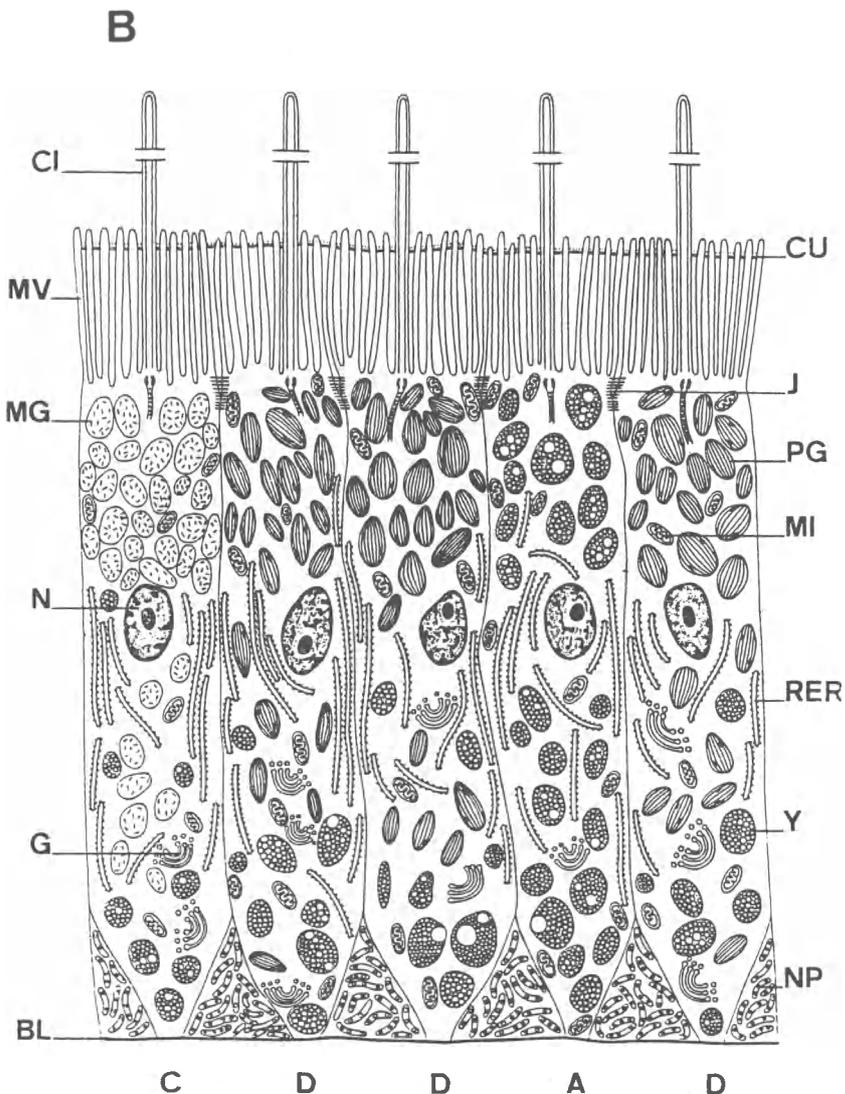


Figure 6. (Continued). Diagrammatic representation of the cells of the ciliary cap (A) and of the adhesive pit (B) of the attachment complex in the doliolaria larva of the comatulid crinoid *Antedon bifida* (modified from Jangoux & Lahaye 1990). A = Type A ciliated non-secretory cell, B = Type B ciliated non secretory cell, BL = basal lamina, C = Type C ciliated secretory cell, CI = cilium, CU = cuticle, D = Type D ciliated secretory cell, G = Golgi complex, J = septate junction, MG = mucous secretory granule, MI = mitochondria, MV = microvilli, N = nucleus, NP = nerve plexus, PG = proteinic secretory granule, RER = rough endoplasmic reticulum, Y = yolk granule.

stratum by a basal adhesive disc (Mladenov & Chia 1983, Lahaye & Jangoux 1987). In *Antedon bifida*, the disc epidermis is strikingly different from the epidermis of the doliolaria attachment complex from which it derives (Lahaye & Jangoux 1991). The cystidean disc epidermis is made up of a single cell type that is neither ciliated nor secretory. Yet the disc adheres strongly to the substratum through a solid cement. This cement consists of the remnants of the proteinaceous material secreted by the Type D ciliated secretory cells of the doliolaria adhesive pit (Mladenov & Chia 1983, Lahaye & Jangoux 1991).

### 3.1.2 *Asteroidea*

The larval stages of asteroids are the bipinnaria stage and the brachiolaria stage. The latter possesses special adhesive structures: the brachiolar arms and an adhesive disc (Dawydoff 1948, Strathmann 1978). The adhesive disc is at the anterior end of the larva, with a pair of brachiolar arms lateral and posterior to it and a third single arm anterior to it (Fig. 7).

The brachiolar arms are tubular structures whose center is occupied by an extension of the coelom (Barker 1978). They are made up of four tissue layers: an inner mesothelium, a connective tissue layer, a nerve plexus and an outer epidermis. Each brachiolar arm terminates in a crown of adhesive papillae where both the epidermis and the nerve plexus are greatly thickened. The papilla epidermis consists of five cell types: three types of secretory cells (A, B and C), one type of non-secretory ciliated cells (= secretory cells), and one type of support cells (Barker 1978). Type A secretory cells are the most numerous. These cells bear an apical cilium and are filled with electron-dense heterogeneous secretory granules about 1  $\mu\text{m}$  in diameter. The histochemical reactions of the secretory granules suggest they contain neutral mucopolysaccharides. Also common in the adhesive papillae are Type B secretory cells with smaller homogeneous granules (150-450 nm in diameter) of somewhat variable electron density. Type C secretory cells are much less common than the two other types of secretory cells, and occur only around the outer margin of the papilla. The cytoplasm of these cells contains spherical granules (about 1.5  $\mu\text{m}$  in diameter) enclosing moderately electron-dense material. Support cells, the second most abundant cell type of the papilla, are distributed uniformly within the papilla, whereas sensory cells are clustered towards the tip of the papilla.

The adhesive disc is a round, concave structure lying between the three brachiolar arms. It is made up of columnar epidermal cells on the ventral side of the pre-oral lobe (Barker 1978). These cells comprise secretory cells and support cells. The former are filled with round, membrane-bound secretory granules ranging from 1.5 to 3  $\mu\text{m}$  in diameter.

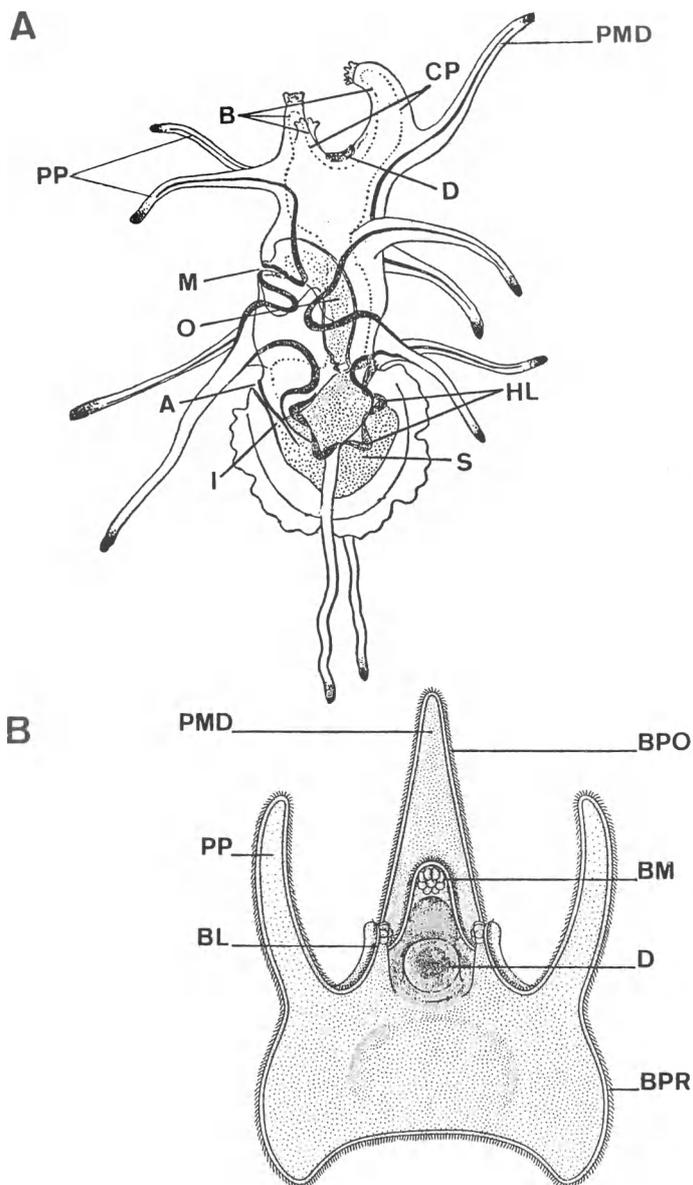


Figure 7. Asteroid brachiolaria larva. A) general view (*Asterias forbesi*) (modified from Mead 1899). B) Detailed view of the larva anterior end (*Asterias rubens*) (original). A = anus, B = brachiolar arms, BL = lateral brachiolar arm, BM = median brachiolar arm, BPO = postoral ciliary band, BPR = preoral ciliary band, CP = preoral coelom, D = adhesive disc, HL = hydrocod lobes, I = intestine, M = mouth, O = oesophagus, PMD = median dorsal process, PP = preoral process, S = stomach.

These granules enclose a moderately electron-dense homogeneous material that was demonstrated histochemically to be proteinaceous.

During settlement, the brachiolar arms are used in attaching brachiolaria larvae temporarily on the bottom during exploration, whereas the adhesive disc is used in a more permanent attachment during resorption of the larval body at metamorphosis (Strathmann 1978, Barker 1977, 1978). On touching the substratum, the larva orients itself with the ventral side down and attaches by one or two of the three brachiolar arms, contact being by the crown of adhesive papillae on the tip of each arm. The larva then 'walks' across the substratum by successively attaching and detaching its brachiolar arms (Barker 1977). The adhesive papillae could therefore function as a duo-gland adhesive system, the Type A secretory cells being adhesive and the Type B secretory cells being deadhesive. Indeed, these cells are strikingly similar to podial secretory and neurosecretory-like cells, respectively. In the presence of adverse stimuli or the absence of positive stimuli the larva swims off. When, however, metamorphosis ensues on the substratum, the brachiolar arms are gradually splayed out, bringing the adhesive disc in close contact with the substratum (Barker 1977). Its secretory cells then release their proteinaceous cement and attachment becomes permanent.

### 3.2 Cuvierian tubules

Cuvierian tubules are conspicuous intracoelomic caeca found in some species of aspidochirote holothuroids. They are rather short, whitish tubules that occur generally in great numbers and attach to the basal part of the left respiratory tree. In some species of the genera *Holothuria* and *Bohadschia*, Cuvierian tubules act as defensive structures. Irritated holothuroids expel them through the anus. The expelled tubules lengthen, become sticky and rapidly immobilize most organisms with which they come into contact (VandenSpiegel 1993).

The mechanism of discharge and fine structure of the Cuvierian tubules has been described by VandenSpiegel & Jangoux (1987) in *Holothuria forskali*. In this species, discharge of tubules results from the complementary and simultaneous processes of tubule expulsion and elongation. Both processes are triggered by the opening of the anus of contracted holothuroids. The anal opening results in forceful and active expulsion of water from the respiratory trees and the rupture of the cloaca with the subsequent expulsion of coelomic fluid containing a few elongating tubules that exit the cloaca blind end first. The tubules remain connected to the base of the respiratory tree at first but later are autotomized. In seawater the tubules elongate to 20 times their original length.

They become sticky only after expelled, providing they contact a solid surface.

Cuvierian tubules consist of an outer mesothelium and an inner epithelium encompassing a thick connective tissue layer (VandenSpiegel & Jangoux 1987). The outer part of the connective tissue includes muscle fibers. These tissue layers are continuous with the corresponding layers of the left respiratory tree. The mesothelium is the tissue layer involved in the adhesive process. In quiescent tubules, it is a pseudostratified epithelium made up of two cell layers, viz. an apical layer of adluminal cells and a basal layer of granular cells (Fig. 8). Together both cell types form conspicuous transversal folds that penetrate the underlying connective tissue. Adluminal cells are *T*-shaped, with the basal portion of the *T* penetrating deeply into the tubule connective tissue. Their apical parts, bearing a single cilium, line the coelomic cavity. The apical cytoplasm encloses conspicuous mucous granules averaging 2-4  $\mu\text{m}$  in diameter. Granular cells form extensive penetrations into the connective tissue compartment. These penetrations are *V*-shaped, with the *V* surrounding the basal processes of the adluminal cells. Granular cells are filled with densely-packed membrane-bound granules averaging 1-2  $\mu\text{m}$  in diameter that are filled with an homogeneous electron-dense matrix. Histochemical tests indicate that these granules lack mucosubstances but contain both protein and lipid fractions. When tubules elongate, the adluminal cells disintegrate, with their mucus contents being released and covering the tubule outer surface. The granular cells, now unfolded, thus become outermost on the tubule. These dump the contents of their granules when the elongated tubule comes into contact with a surface, resulting in the tubule adhering to the surface (VandenSpiegel & Jangoux 1987).

Adhesion of Cuvierian tubules in *Holothuria forskali* has been studied mechanically and biochemically by Müller et al. (1972) and Zahn et al. (1973). According to these authors adhesion is due to a proteinic material that could be under enzymatic control. However, they do not specify either the type of enzyme involved or the localization of the enzyme and the substrate in the tubule. Zahn et al. (1973) measured an adhesive force of  $0.25 \times 10^5 \text{ N/m}^2$  for Cuvierian tubules attached to paraffin wax. They also reported that tubules adhere more strongly to glass than to paraffin wax.

#### 4 COMPARISON WITH OTHER MARINE INVERTEBRATES

Many marine benthic organisms are equipped with structures that allow them to attach to the substratum. These structures are involved in mechanical attachment and/or chemical attachment. The way the former op-

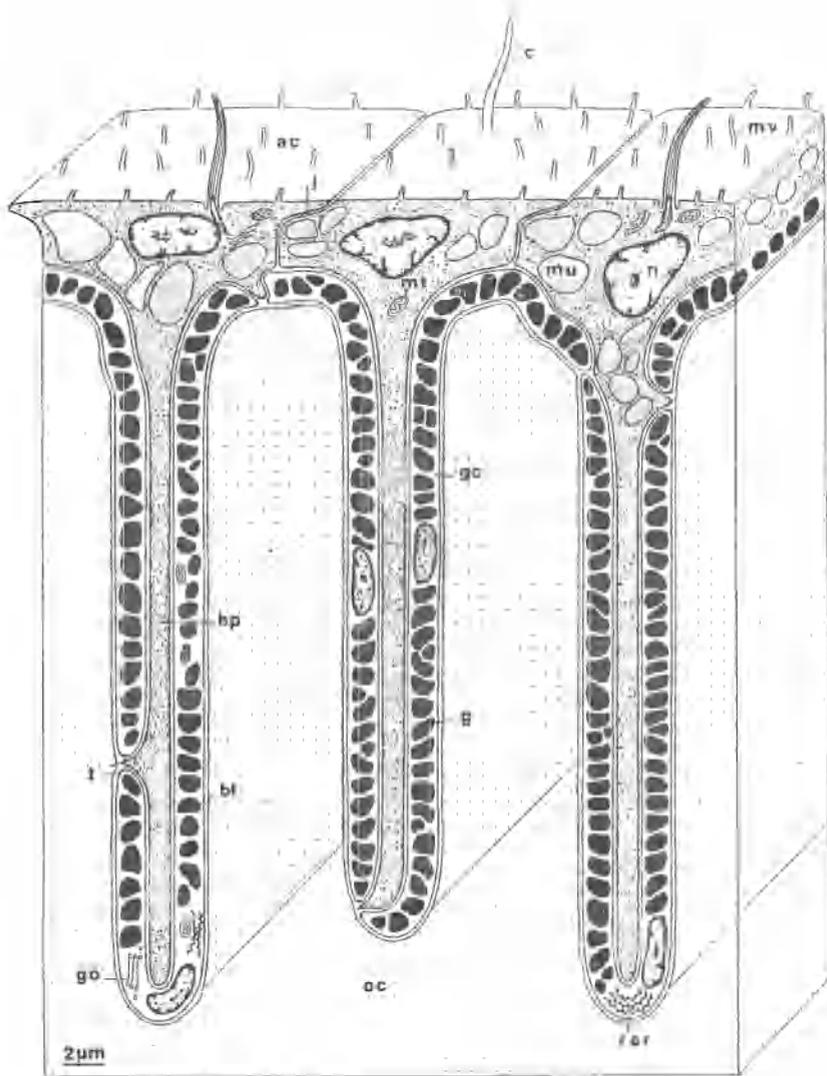


Figure 8. Diagrammatic representation of the mesothelium of a quiescent Cuvierian tubule of the holothuroid *Holothuria forskali* (from VandenSpiegel & Jangoux 1987). ac = adluminal cell, bl = basal lamina, bp = basal process of an adluminal cell, c = cilium, g = secretory granule, gc = granular cell, go = Golgi complex, j = septate junction, mt = mitochondrion, mu = mucus granule, mv = microvillus, n = nucleus, oc = outer connective tissue layer, rer = rough endoplasmic reticulum, t = thickening of the cell membrane.

erate is generally obvious (as in the case of hooks or suckers), whereas the functioning of the latter remains enigmatic.

The term adhesion is generally used to describe an attachment process mediated by adhesive secretions. Three types of adhesion may be distinguished: 1) temporary adhesion allowing an organism to attach strongly but momentarily to the substratum (e.g. the adhesion of echinoderm podia); 2) transitory adhesion permitting simultaneous adhesion and movement along the substratum (e.g. the foot secretions of some molluscs); and 3) permanent adhesion involving the secretion of a cement (e.g. the attachment of barnacles on rocks) (Tyler 1988). These three types of adhesion do not have the same purpose and use different adhesive systems.

*Temporary adhesion* allows organisms to attach momentarily to a substratum. This type of adhesion generally involves duo-gland structures, including two types of secretory cells (viz. cells releasing an adhesive secretion and cells releasing a de-adhesive secretion). These duo-gland adhesive structures are found very frequently in small invertebrates inhabiting the interstitial environment, for example Turbellaria (Tyler 1976); Gastrotricha (Tyler & Rieger 1980); Nematoda (Adams & Tyler 1980); and Polychaeta (Gelder & Tyler 1986). Among marine invertebrate adhesive structures, they are the closest morphologically to echinoderm podial adhesive systems. In every species studied, the adhesive structures contain two types of closely associated secretory cells. Cells of the first type are specialized epidermal cells similar to echinoderm secretory cells. They are filled with homogeneous secretory granules in turbellarians and gastrotrichs (Tyler 1976, Tyler & Rieger 1980), and with dense-cored granules in nematodes and polychaetes (Martin 1978a, Adams & Tyler 1980, Gelder & Tyler 1986). These cells release the adhesive material. Cells of the second type are derived from sensory nerve cells and resemble echinoderm neurosecretory-like cells. They enclose numerous small electron-dense secretory granules. In several turbellarians, they release their granules through a pore adjoining the secretory pore of the adhesive cell (Tyler 1976). In all groups, these cells are considered to be deadhesive in function. Unfortunately, as far as the chemical composition of the secretions is concerned, the small size of duo-gland structures in invertebrates of the meiofauna has precluded any kind of biochemical analysis (Tyler 1988).

A duo-gland adhesive system has also been described in the captacula (i.e. the food-collecting tentacles) of scaphopod molluscs (Byrum & Ruppert 1994), widening further the distribution range of this adhesive system in marine invertebrates. However, duo-gland adhesive systems do not seem to be the only adhesive systems involved in temporary adhesion. In a few taxa, structures containing only one type of secretory cell

attach and detach quickly. Such adhesive systems occur in some turbellarians (Tyler 1976, Ehlers 1989), gastrotrichs (Tyler et al. 1980) and nematodes (Lippens 1974). These structures are best developed in cnidarians. Medusae of several species of hydrozoans possess adhesive tentacles that can attach and detach repetitively (Bouillon 1968, Singla 1977, Honegger 1984). In all these species, the detachment process is not well understood but could be purely mechanical (Tyler et al. 1980, Honegger 1984).

*Transitory adhesion* allows simultaneous adhesion and movement along a substratum, the animals attaching to the substratum by a viscous film they leave behind as they move. This type of adhesion is characteristic of invertebrates moving along the substratum by ciliary gliding, mostly small soft-bodied invertebrates such as turbellarians, nemertines, gastrotrichs or archiannelids (Martin 1978b). Larger animals like sea anemones and gastropod molluscs also use transitory adhesion, moving by means of waves of muscular contractions running along their foot. In the limpet *Patella vulgata*, the material involved in transitory adhesion comes from six types of secretory cells located in the foot (Grenon & Walker 1978). This material is a protein-carbohydrate complex with the two moieties linked by electrovalent bonds. The carbohydrate moiety is in the form of sulphated acid mucopolysaccharides (Grenon & Walker 1980). It possesses visco-elastic properties and thus behaves like an elastic solid during adhesion and like a viscous fluid during locomotion (Denny 1980).

A.M. Smith (1991, 1992) has proposed that stationary limpets may use two different attachment mechanisms. They preferentially use sucker-like mechanical attachment when they are stationary for a short period of time, and chemical attachment when stationary for a long period of time. The latter gives by far the greater adhesive strength to the limpet. At the end of the stationary period, the limpet must detach before it resumes crawling. This behaviour is close to temporary adhesion. Similarly, the release of the disc in some species of sea anemones could be due to the secretion of a deadhesive substance (Ellis et al. 1969).

*Permanent adhesion* involves the secretion of a cement and is characteristic of sessile organisms staying at the same place throughout their life. Sessile organisms have representatives in numerous taxa: sponges, cnidarians, cirripede crustaceans, bivalve molluscs, polychaetes, bryozoans and tunicates (Crisp 1974b, Lindner 1984). Barnacles and mussels are the most studied. The adhesive systems involved in permanent adhesion comprise generally only one type of secretory cell, or, when more than one type of secretory cells are present, only one is involved in adhesion (Walker 1970, Tamarin et al. 1976, Waite 1983a). The adhesive material

is exclusively proteinic and rich in phenolic residues. It is secreted as a fluid, and then solidifies gradually to become a permanent cement. This solidification is due to the formation of cross-links under the action of a phenoxidase enzyme. The phenolic residues are oxidized into *o*-quinones which then react with amine residues (e.g. lysines) of other proteins to form inter-molecular covalent bonds (Walker 1972, Walker & Youngston 1975, Waite 1983b, 1987, Lindner 1984). This type of adhesion may be similar to the one brought into play during the attachment of holothuroid Cuvierian tubules.

*Adhesion of larvae* in numerous benthic marine invertebrates proceeds in two successive stages using two of the three types of adhesion, non-permanent adhesion (temporary or transitory) and permanent adhesion. These larvae, when searching for a favourable site for metamorphosis, explore the substratum and use an initial secretion (generally a mucopolysaccharide) to attach. Depending on the taxon, the larvae may attach and detach repetitively (temporary adhesion) like the brachiolaria larvae of asteroids, or they may adhere loosely to the substratum while they move (transitory adhesion) like the doliolaria larvae of crinoids. If the substratum is not appropriate, the larvae detach and resume swimming. If appropriate, they cement themselves permanently to the substratum using a second type of secretion, which is proteinaceous, and start their metamorphosis (Chia & Rice 1978, Crisp 1984). This permanent fixation occurs in all larvae irrespective of whether they use temporary or transitory adhesion during their exploratory phase and, indeed, permanent adhesion is encountered in both brachiolaria and doliolaria larvae.

*Adhesive strengths* have been measured for several marine invertebrates from a wide range of taxa, on a wide range of substrata. Table 4 presents only adhesive force measurements made on glass substrata, so valid comparisons can be made. Adhesive force values of organisms using permanent adhesion are usually higher than those of organisms using non-permanent adhesion (temporary or transitory). The single adhesive strength measurement made on asteroid podia ( $1.7 \times 10^5$  N/m<sup>2</sup>, Paine 1926) fits well within the tenacities of marine invertebrates that use non-permanent adhesion. The adhesive strength of holothuroid Cuvierian tubules has not been measured on glass but on paraffin wax ( $0.25 \times 10^5$  N/m<sup>2</sup>, Zahn et al. 1973). The tenacities of mussel byssus on paraffin wax and glass are  $0.13 \times 10^5$  N/m<sup>2</sup> and  $3.16 \times 10^5$  N/m<sup>2</sup>, respectively (Young & Crisp 1982). Using the same proportion, the tenacity of Cuvierian tubules on glass could be about  $6 \times 10^5$  N/m<sup>2</sup>, a value that compares well with other permanent adhesion strengths.

Table 4. Comparison of the mean tenacity of some marine invertebrates on smooth glass.

Taxa	Species	Structure involved in adhesion	Type of adhesion	Tenacity ( $\times 10^5$ N/m <sup>2</sup> )	References
Cnidaria	<i>Metridium senile</i>	Foot	Transitory	0,43	Young et al. 1988
Anthozoa	<i>Actinia equina</i>	Foot	Transitory	0,19	Young et al. 1988
Mollusca Gasteropoda	<i>Patella vulgata</i>	Foot	Transitory	2,28	Grenon & Walker 1981
Mollusca Bivalvia	<i>Mytilus edulis</i>	Byssus	Permanent	3,16 (February) 7,5 (June)	Young & Crisp 1982
Crustacea Cirripedia	<i>Semibalanus balanoides</i> (cyprid larva)	Antennules	Temporary	0,98	Yule & Walker 1987
	<i>Semibalanus balanoides</i> (adult)	Base	Permanent	2,3	Yule & Walker 1987
	<i>Balanus crenatus</i>	Base	Permanent	5,2	Yule & Walker 1987
Echinodermata Asteroidea	<i>Asterias vulgaris</i>	Podia	Temporary	1,7	Paine 1926
Echinodermata Holothuroidea	<i>Holothuria forskali</i>	Cuvierian tubules	Permanent	6*	Zahn et al. 1973

\*Estimated value (see text).

## 5 CONCLUSIONS AND PROSPECTS

Adhesion is a way of life in the sea. Indeed, representatives of bacteria, all lower plants from unicellular algae to macroalgae, and all animal phyla living in the sea attach permanently, transitorily or temporarily to surfaces, including other organisms. However the adhesion mechanism and detailed chemical nature of the adhesives used are largely unknown (Waite 1983a, Walker 1987). Over the past twenty years or so there has been an upsurge of interest in the adhesion mechanisms of so-called 'fouling' organisms. These organisms attach to man-made surfaces such as ship hulls, oil rigs, intake pipes of power stations and heat exchangers (Haderlie 1984, Walker 1987, Baier & Meyer 1991). The interest also centres on the fact that many marine organisms produce adhesives, which, as they are released and act under water, may find applications in the medical and dental fields (Dahlquist 1977, Walker 1987, Baier & Meyer 1991).

Familiar examples of marine macrofouling organisms are macroalgae, barnacles, mussels, and tubeworms (Lindner 1984, Walker 1987). All these organisms, in the adult form, use permanent attachment to cement onto the substratum, hence the large number of studies on permanent adhesives and structures involved in permanent adhesion (see e.g. Waite 1983a, 1987, Yule & Walker 1987). However, in the larval form, they use firstly temporary adhesion to explore substrata. A better understanding of temporary adhesion might lead to methods for interfering with the process of adhesion and therefore controlling the settlement of fouling organisms (Crisp 1974a). The small size of larval adhesive structures has precluded any biomechanical or biochemical studies on temporary adhesion. The study of macroinvertebrate adhesive systems is, therefore, a promising way of understanding temporary adhesion.

Of all macrobenthic organisms, echinoderms have exploited temporary adhesion most efficiently. In echinoderms, adhesive systems are usually associated with the podia and are involved in locomotion, attachment, feeding, or burrowing. They are duo-glandular, enclosing secretory cells releasing an adhesive material and neurosecretory-like cells releasing a deadhesive material. However, the chemical compositions of these materials are still largely unknown. Future studies should isolate and purify both adhesive and deadhesive substances, define their physico-chemical characteristics, and elucidate their structures. In addition, more adhesive force measurements made on echinoderms from different classes in different conditions are needed urgently. Such information, together with the morphological data, would provide the necessary basis for understanding how echinoderm adhesive systems are used in temporary adhesion.

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