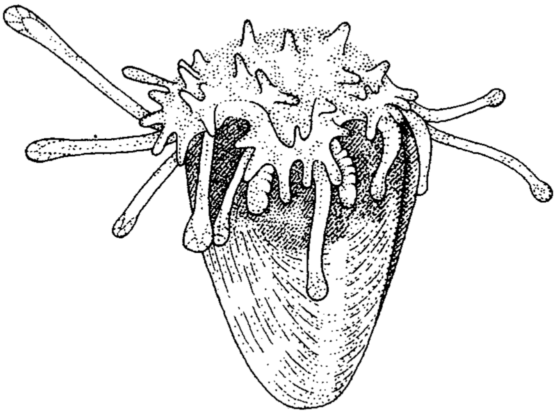
MICHEL JANGOUX & JOHN M. LAWRENCE (EDITORS)

ECHINODERM NUTRITION

A.A. BALKEMA PUBLISHERS / ROTTERDAM

ECHINODERM NUTRITION



Juvenile *Asterias vulgaris* about 2 days old devouring a clam (from Mead 1901).

ECHINODERM NUTRITION

Edited by

MICHEL JANGOUX
Université Libre de Bruxelles, Belgium

JOHN M. LAWRENCE
University of South Florida, Tampa, USA

A.A.BALKEMA / ROTTERDAM / 1982

ISBN 90 6191 080 3

Distributed in USA & Canada by MBS, 99 Main Street, Salem, NH 03079, USA
Printed in the Netherlands

TABLE OF CONTENTS

PART ONE: FOOD AND FEEDING MECHANISMS

PART TWO: DIGESTIVE SYSTEMS

PART THREE: PHYSIOLOGY AND BIOCHEMISTRY

PART FOUR: NUTRITION DURING DEVELOPMENT

PART FIVE: EFFECTS OF FEEDING ON THE ENVIRONMENT

FOREWORD

Living systems are open ones thermodynamically, and must obtain energy and matter to maintain themselves through time. This is a basic principle of biology. Understanding the ways in which living systems obtain and utilize nutrients is thus of fundamental importance. We have taken a broad view of nutrition deliberately, not confining ourselves to the requirements for, and utilization of nutrients. We begin with the perception of food and all feeding, digestive, and absorptive processes which lead to the uptake of nutrients, and continue through the ecological effects of feeding. A necessary consequence of feeding is the removal of matter and energy from the system which often involves the predation of other animals and plants. The removal of prey individuals from the system and the change in the physical and chemical state of biological material as a result of nutritional action both have environmental consequences.

The purpose of this book is to present the state of knowledge concerning nutrition and point out directions for future work for the Echinodermata, an ancient group which shows great diversity in form and function, and whose feeding activities can have great environmental impact. The echinoderm classification proposed in Moore's *Treatise on Invertebrate Paleontology* has been followed throughout this book.

We sincerely thank all the contributors for their efforts. Thanks are also due to those who helped during the editorial work, especially N.Biot, J.Harray, and M.Klinkert (Laboratoire de Zoologie, Université Libre de Bruxelles). We are grateful to the 'Fondation Roi Léopold III' and to the 'Ministère de l'Education nationale de Belgique' for financial support.

The editors

PREFACE

It is timely that a book on echinoderm nutrition should appear. In the present volume echinoderm metabolism and many other phases of echinoderm nutrition are summarized and evaluated, many for the first time. A much more meaningful concept of the overall nutrition of echinoderms will emerge from a knowledge of perception of food, environmental effects of feeding, structure of the digestive organs, digestion, absorption, translocation and assimilation of nutrients, excretion and metabolism. The present volume should be awaited with anticipation not only by those interested in echinoderms, but also by those wishing to compare the nutrition of echinoderms with the nutrition of animals in other phyla. The primitive nature of the echinoderms makes them of special interest in this regard as a background for comparative studies on the nutrition of animals. In addition, a summary of this type will point out the deficiencies in our knowledge and thereby bring to the attention of younger scientists some of the problems they might fruitfully attack. There are no final answers in a treatise and part of its value is the stimulus it provides for another generation of researchers. It is my hope that this treatise will entice others to experience the joy of collecting from the ocean, working with the organisms at the seaside, and solving some aspect of the nutrition of echinoderms.

Arthur C. Giese
Professor Emeritus of Biology, Stanford University

1. FOOD AND FEEDING MECHANISMS

N. A. SLOAN & ANDREW C. CAMPBELL

1

PERCEPTION OF FOOD

The turbidity of inshore waters and the irregularity of much of the sea-bed limit the effectiveness of sight as a major sensory modality for many benthic marine invertebrates (Mackie 1975). Vision is, however, used extensively by a few specialised groups such as cephalopods (Wells 1978) and crustaceans (Waterman 1961, Hazlett 1972). Nicol (1967) did not consider that the ability to hear was widespread among marine invertebrates although some exceptions occur amongst the crustaceans (Salmon & Horch 1972, Meyer-Rochow & Penrose 1976). By contrast it seems that the transfer of information chemically either by contact or by water is particularly suitable for aquatic animals. Carthy (1958) pointed out that the usefulness of chemoreception is greatly enhanced when given directionality by current induced gradients. A further advantage is that only minute quantities of a chemical need be used to release a behavioural sequence (Lenhoff & Lindstedt 1974). Mackie & Grant (1974) among others, believed that chemoreception amongst marine invertebrates was a subject the importance of which 'cannot be overemphasised'. Such awareness had not escaped earlier workers, for example Pearl (1903), who wrote 'one of the most important factors in the sum total of activities of any aquatic organism is its reactions to chemical substances'.

Modern techniques, particularly in the realm of electrophysiology, have led to a more accurate analysis of the processes of transduction and integration of sensory activity in nervous systems, but as Ramsay (1968) pointed out, chemoreception appears to lag behind on research effort by comparison with other sensory modalities, e.g. vision. It is encouraging that more recently Lenhoff & Lindstedt (1974) indicated some improvement of the situation concerning chemoreception research methods and objectives so that the paradox of intensity of investigation on the one hand and biological significance on the other many be resolving (Kittredge *et al.* 1974). Concerning topics of inter-specific chemoreception in marine invertebrates generally, food detection has the best coverage (Passano 1957, Kohn 1961, Laverack 1963, Lindstedt 1971, Lenhoff & Lindstedt 1974). In a review of feeding, digestion and nutrition of all echinoderms, however, Ferguson (1969a) devoted only a very minor portion to 'Chemosensitivity to food', a measure of how poorly understood the field of echinoderm chemoreception has been.

1. CHEMORECEPTION IN ECHINODERMS RELATED TO THEIR STRUCTURE AND LIFE STYLE

Echinoderms have unusual anatomical arrangements linked with peculiar physiological and behavioural ones which have considerable effects upon food perception and feeding. The form of symmetry, especially in relation to the lack of a head, the distribution of sensory and nervous elements, and the distribution of locomotor units are of paramount importance.

There is little doubt that the first echinoderms were sedentary, if not sessile, suspension feeders (Nichols 1969). The water vascular system with its protrusible hydraulic tube-feet probably arose as a respiratory system which, because of its arrangement with respect to the mouth, allowed it to fulfil a food collecting role too (Nichols 1969), as in the crinoids. In such animals the pentameric plan is ideal and the lack of a head no disadvantage. Most remaining extant echinoderms have undergone major evolutionary advances. These include the inversion of their bodies with respect to the substrate and the assumption, in some cases, of a superficial bilateral symmetry. Such developments, however, have not led to the universal abandonment of suspension feeding. The inversion of the body allowed the water vascular system to take on an additional function, that of locomotion. Such slow moving or sedentary radially symmetrical animals can receive chemical stimuli emanating from all directions equally well. Moreover, a rounded or disc-like body widely covered with receptor units should provide an ideal mechanism for gross sensory perception and analysis by simultaneous monitoring of stimulus intensity at different positions on its surface.

Adult echinoderms are generally sluggish and creep slowly over or through the substrate. Some of these remain for a great part of the time in one place, and only a few species, all holothuroids, have become pelagic. Judging by the success of some modern free-living echinoderms, whose populations may dominate the environment (Nichols 1975), the pentameric plan has not been a serious limitation on free life. With the water vascular system providing locomotion, free life in a number of styles (e.g. creeping, burrowing, crevice dwelling) became possible and with this possibility the chances of filling a variety of niches as grazing herbivores, omnivores, predators and carrion feeders. All these types of feeding method rely to some extent on chemical or physical perception and the means to orientate to and then take in the food.

Errant echinoderms must move to get their food. It is important that they do so efficiently. This is the essence of evolutionary pressure which has produced the various habits and life styles displayed by the errant echinoderms.

The most striking feature of the echinoderm nervous system is the lack of a brain. Sense organs are rare in this group and transduction of environmental stimuli is generally a function of single unspecified cells widely distributed over most of the body surface. For example, Cobb (1968a) suggests that most epithelial cells of echinoids have neuronal connections and act as transducers, but this suggestion awaits experimental proof. So far, no specific region of the nervous system with responsibility for integration of primary sensory modalities has been designated.

The echinoderm nervous system has been reviewed by J.E.Smith (1950, 1965) and by Pentreath & Cobb (1972). There are three essential parts, although these may not be present in all echinoderms. They are:

1. The ectoneural system, mainly sensory, and occurring in all classes except crinoids.
2. The hyponeural (Lange's nerve in asteroids) lacking in echinoids and holothuroids where its motor function is taken over by part of the ectoneural system.
3. The apical system, important in crinoids in which it is motor and innervates the viscera, but poorly developed in asteroids. This system lacks in the other classes.

Prime responsibility for chemoreception is taken by the ectoneuronal system. Structurally it is divided into two parts. Associated with each ambulacrum is a well-developed radial nerve cord. It provides the major afferent pathways from the receptors of the test and ambulacrum, and in groups where the hyponeural system is lacking it provides motor pathways to the tube feet too. Each radial cord is connected with the others via a circum-esophageal nerve ring which provides a route for inter-radial integrative activities. In echinoids and asteroids, where there is a good covering of epithelial cells overlying the skeleton, a well-developed basi-epithelial nerve plexus constitutes the second part of the ectoneural system (Bullock 1965, Campbell 1973). The principal role of this plexus is to receive nervous impulses arising from the multiplicity of sensory cells and to pass them where applicable to the radial nerve cords, and to co-ordinate the activities of the test appendages. In the remaining three classes the basi-epithelial nerve plexus is less well-developed; there are fewer test appendages and, with the exception of holothuroids, the epithelium is often scanty and abraded.

Analysis of sensory and motor phenomena in the plexus has been hindered by technical difficulties. The small diameter and diffuse nature of the component axons prevent intracellular recording. Also the presence of free crystals of calcite, even away from the skeleton, makes probing with fine instruments difficult. Within the radial cords, however, some progress has been made using gross techniques such as wick electrodes (Sandeman 1965). Electrophysiological proof for the hypothesis of chemoreception in echinoderms, therefore, is in a state of conjecture.

The hyponeural system is found in asteroids and ophiuroids where it co-ordinates motor activities of the tube-feet and ampullae and is important in locomotion. The locomotory tube-feet are hydraulic organs which possess muscles allowing stepping movements and retraction. In most asteroids, echinoids and holothuroids they are suckered which assists with adhesion, but in ophiuroids they are suckerless and not important for movement. A fuller account is given in Nichols (1966, 1969). Tube-feet can be intimately involved in the feeding process. In some cases they are well-known as food gatherers. Their implication in food detection, mentioned later in the organs of chemoreception section, is not surprising because as extensions of the body wall they are cloaked with a basi-epithelial plexus.

The development of the anatomical resources of the various classes (compared with their habitat, life style, and source of food in table 1) suggests the potential for food detection in various echinoderm groups. Those groups which lack a well-developed sensory component in the basi-epithelial nerve plexus may be restricted to a semi-sedentary life like the filter-feeding crinoids or the deposit-feeding holothuroids. Interestingly, although ophiuroids, with their relatively massive skeleton and subsequently reduced basi-epithelial plexus, are mostly suspension-feeders, some are polyphagous (Fontaine 1965, Chartock 1972, Dearborn 1977) and responsive to chemical stimuli. The increase in the sensory component and motor sophistication has allowed for the development first of relatively unselective omnivorous feeding as in regular echinoids, and secondly a more selective predatory life as in some asteroids, where strong dietary preferences may be encountered.

2. PHYSICAL PERCEPTION OF FOOD AND FEEDING

Large scale movements or aggregations of asteroids and echinoids have been related to food availability (Dana *et al.* 1972, Lawrence 1975a, Grassle *et al.* 1975, Glynn 1976, Sloan 1977, Mattison *et al.* 1977, Garnick 1978), whereas the presence of suspension feeders is more strongly related to current conditions (Warner 1971, Fedra *et al.* 1976, Meyer & Lane 1976, Meyer & Macurda 1977) which bring the food to the awaiting masses.

There are a number of instances where purely physical characteristics of the environ-

Table 1. Relationship of anatomical and ecological characteristics of extant adult Echinodermata

Class	Order	Lifestyle	Habitat	Feeding mechanism	Symmetry	Basi-epithelial nerve plexus and sense organs	Water-vascular system
Crinoidea	Articulata	Sedentary or sessile	Benthic, usually on hard ground	Suspension feeders using tube-feet and mucus	Radial	Poorly developed with no sense organs as such	Not employed in locomotion, but used in feeding and respiration
Asteroidea	Platyasterida Paxillosida Valvatida Spinulosida Forcipulatida	Many errant; few sedentary	Benthic on or in soft ground; on hard ground	Voracious carnivores; some omnivores and detrital feeders	Radial	Well developed in many cases; some simple sense organs, e.g. optic cushion	Well developed for locomotion, burrowing, respiration and sensory perception
Ophiuroidea	Oegophiurida Phrynophiurida Ophiurida	Some sedentary; some errant	Benthic on or in soft ground; on hard ground	Diverse: suspension feeders; surface film feeders; detrital feeders; carrion feeders; carnivores	Radial	Poorly developed in most cases	Not employed in locomotion, but used in feeding and respiration
Echinoidea	Cidaroida Diadematoida Echinoida	Some sedentary; some errant	Benthic, usually on hard ground	Most graze algae or encrusting animals: some catch suspended particles	Radial	Well developed sense organs in pedicellariae	Employed in locomotion, food handling, covering and various other activities
	Holectypoida Clypeasteroida	Sedentary: many burrow	Sands and gravels	Ingest food particles occurring in or on substrate	Bilateral	Well developed but virtually no sense organs	Employed in burrowing, respiration and probably sensory
	Holasteroida Nucleolitoida Cassiduloida Spatangoida	Sedentary burrowers	Sands and gravels	Ingest substrate and associated organic material	Bilateral	Well developed but virtually no sense organs	Very specialised in some groups; employed in burrow-maintenance, respiration and various other activities
Holothuroidea	Dendrochirotida Dactylochirotida Aspidochirotida Elasipodida Molpadida Apodida	Almost all benthic and sedentary: a few species are pelagic	Hard and soft ground crevice dwellers, surface dwellers and pelagic	Suspension or deposit feeders using modified tube-feet	Radial or bilateral	Poorly developed	Employed in locomotion, feeding and respiration, and various other activities

ment control the feeding activities of echinoderms. In the case of irregular echinoids (Ferber & Lawrence 1976, Gladfelter 1978) and burrowing holothuroids (Rhoads & Young 1971, Lawrence & Murdoch 1977) the quality of the substrate as an amenable burrowing medium may affect the distribution and feeding activities of infaunal species. Wave action can affect the distribution and feeding activities of echinoids (Dart 1972, Lawrence 1975a: 261, Russo 1977) and asteroids (Ormond *et al.* 1973, Menge 1974, Dayton *et al.* 1977), as can exposure to air (Landenberger 1969).

The effects of physical characteristics such as shape and rugosity on highly mobile predatory asteroids have been little considered. Although asteroids can demonstrate a tactile discrimination ability (e.g. *Asterias rubens:* Sokolov 1961, in Valentinčič 1978), they are more motivated by chemical cues than physical shapes of potential prey. In perhaps the only prey-form recognition experiments, Valentinčič (1975) could find only a limited ability of *Marthasterias glacialis* to discriminate between cleaned gastropod shells and similar sized stones.

Filter-feeding echinoderms such as most crinoids, ophiuroids, and dendrochirote holothuroids are markedly rheophilic. Responses to current influence population distribution and orientation of feeding apparatus rather than a chemosensory orientation. An exception among the dendrochirote holothuroids could be *Psolus chitinoides,* described as an active suspension feeder with a potential chemosensitivity in a laboratory study by Fankboner (1978). On the other hand *in situ* observations by Könnecker & Keegan (1973) on *Pseudocucumis mixta,* by Hunter-Rowe *et al.* (1976) on *Thyone fusus,* and by Olscher & Fedra (1977) on *Cucumaria planci* all suggest a strongly rheophilic component in the feeding activities of these holothuroids. The random nature of the tentacle activity of other cucumarids like *Cucumaria elongata* by Fish (1967) and *C.frondosa* described by Sutterlin & Waddy (1976) suggests that once the animal orientates itself (to current) the actual feeding rhythm is spontaneous and not environmentally cued, at least in the short term.

Many shallow-water unstalked crinoids (Meyer 1973a, Meyer & Lane 1976, Meyer & Macurda 1977) as well as deep-sea stalked species (Macurda & Meyer 1974, 1976, Welsh 1978) are rheophilic in the orientation of their filtering pinnulate arms. Currents probably are the prime stimulus to feeding in these animals as there is very little mention of chemoreception in crinoids. Although numerous authors suggest chemoreception in filter-feeding ophiuroids, Woodley (1975), Warner & Woodley (1975), Fedra *et al.* (1976) and Wilson *et al.* (1977) state that current orientation is a critical factor in their feeding activities, with reference to *Amphiura* species, *Ophiothrix fragilis, O.quinquemaculata,* and *Ophiocomina nigra* respectively.

The euryalous ophiuroids or basket stars, although plankton-feeders, appear less dependent on current than their sieving relatives. *Gorgonocephalus eucnemis* (Patent 1970), *Astroboa nuda* (Tsurnamal & Marder 1966) and *Astrophyton muricatum* (Davis 1966, Macurda 1976, Meyer & Lane 1976) are all nocturnal feeders that extend their feeding arms to capture large self-mobile plankters. When the plankters contact the arms a rapid coiling action ensues and the food is transferred to the mouth in the tight coil of arms. Feeding posture is perhaps elicited by low light intensities and food capture purely by fortuitous physical contact. An interesting parallel has been described by Campbell *et al.* (1973) in the echinoid *Echinostrephus molaris* from Red Sea reefs. Here algal fragments merely contacting spines trigger food gathering responses.

At this stage, the potentially complementary roles of rheophilic responses to the physical stimuli of current and chemical stimuli of current-born dissolved chemicals or suspended matter are subject to conjecture. Comparison of these types of stimuli could be a fruitful line of research. To our knowledge, only the work of Castilla & Crisp (1970, 1973) on *Asterias rubens* has attempted to examine these two stimuli simultaneously.

3. CHEMICAL PERCEPTION OF FOOD AND FEEDING

Unlike sedentary filter-feeders such as crinoids, other echinoderms which actually seek out their food may resort to one of two methods. Either they can sense their food at a distance using olfaction, or they can rely on a chance encounter. In the latter case, feeding may be initiated if the food is acceptable to the gustatory senses.

Work on asteroids has dominated the field of chemical perception investigations in echinoderms (table 2). It seems certain that gustatory powers exist (Forbes 1841, Hyman 1955, Mauzey *et al.* 1968, Dayton *et al.* 1977), and all these authors report that contact with prey evokes attack and feeding behaviour. In fact, Hyman (1955) stated that 'of all the environmental relations of asteroids, contact is probably the most important' and later, 'asteroids recognise food mainly by contact'. For example, the serie of papers on *Acanthaster planci* has shown that contact with certain chemicals from food extracts soaked into plaster tablets are important in eliciting feeding behaviour (see table 2).

The olfactory ability of echinoderms, particularly asteroids, has been regularly disputed in the literature (see table 2a). The recent generalisation by Dayton *et al.* (1977) that 'asteroids . . . have poor distance-perception, seem to be searchers rather than pursuers and tend to evaluate their prey after capture', is interesting. They, however, observed a population of *Meyenaster gelatinosus* on a wave washed rocky shore where olfactory gradients would be disrupted by turbulent water conditions. In his review on marine invertebrate receptors Laverack (1968a) stated 'the ability to detect food at a distance (usually short) is obviously of great significance to those animals which move slowly (starfish, snails, worms) and yet predate or scavenge'. We tend to agree with this although local environmental conditions, as in Dayton *et al.* (1977), can destroy the effectiveness of asteroid olfaction. Castilla (1972a, b) demonstrated the variable nature of asteroid olfaction by reporting both attraction to whole live mussels, and repulsion to mussel extracts in *Asterias rubens.* The innate variability of echinoderm behaviour in relation to chemoreception will be discussed later.

The significance of the strategy of prey detection in asteroids, whether they are olfactory hunters or fortuitous, incidental feeders could be of importance in evaluating their role as predators in some subtidal marine communities (Mauzey *et al.* 1968, Birkeland 1974, Dayton *et al.* 1974). It is appreciated, however, that olfaction is probably much less important in wave-washed intertidal communities (Dayton 1971, Menge 1972, Menge 1974, Menge & Menge 1974, Paine 1974, Dayton 1975, Paine 1976, Lubchenco & Menge 1978).

By comparison with asteroids, little work has been done on other classes. Work on ophiuroids is largely relegated to anecdotal observations (table 3). Being relatively active these animals are more amenable to behavioural observations than the echinoids, holothuroids, and crinoids.

3.1. *Asteroids*

The nature of the chemical stimuli and short notes on the evidence for or against chemo-

Table 2. Asteroid chemoreception

Species	References	Nature of chemical stimuli	Notes
2a. Positive reports of asteroid chemoreception			
Luidia sarsi	Fenchel 1965	Living and injured ophiuroids	Laboratory observations: damaged ophiuroids were more readily attacked than the live ones
Astropecten aranciacus	Mangold 1908	Fresh fish meat	Laboratory observations: although Preyer (1887) could not show olfaction in this species, Mangold did
Astropecten armatus	Edwards 1969	Live gastropod (*Olivella*) prey	Laboratory observations: asteroid 'quickly runs to' snails placed nearby
Astropecten californicus (= *A. verrilli*)	Hartman 1956	Baited trap with fish meat	Field observations: the asteroids were attracted to bait
Astropecten irregularis	Christensen 1970	Live bivalves, crab, fish and mollusc meat, bivalve extracts	Laboratory observations: the asteroids would orientate to distant food
Astropecten irregularis pentacanthus	Preyer 1886-1887	Fresh crab meat	Laboratory observations: he did find an olfactory ability in this species, although not in *A. bispinosus*
Odontaster validus	Pearse 1969	Prey: the asteroid *Acodontaster*	Field observations: aggregation about food
Id.	Dayton 1972	Prey: the asteroid *Acodontaster*	Field observations: aggregation about food
Id.	Dayton *et al.* 1974	Prey: the asteroid *Acodontaster*	Field observations: aggregation about food
Id.	Dearborn 1977	Fish and seal meat	Field observations: caught in large numbers by the baited traps
Protoreaster lincki	Herdman 1906 (in: Feder & Christensen 1966)	Pearl-oyster beds	Field observations: will move toward oyster beds
Acanthaster planci	Brauer *et al.* 1970	Coral homogenate and washings from live coral which are low molecular weight, water soluble and heat stable compounds	Laboratory observations: simulated stomach eversion and aboral arm curling with tube-feet retraction
Id.	Ormond *et al.* 1973, Ormond & Campbell 1974	Living corals and conspecifics	Laboratory and field observations: stimulated active searching and orientation to chemical stimuli
Id.	Collins 1974, 1975a	Whole coral extract and fractions thereof. Feeding is induced by both high and low molecular weight compounds from coral extract, the former being the more active, Macromolecule not a typical protein being insoluble. The low weight compounds could be amino-acids. The amino-	Laboratory observations: using plaster tablet food models impregnated with extract, settlement and feeding was stimulated

Table 2 (continued)

Species	References	Nature of chemical stimuli	Notes
		acid proline could be responsible for aboral arm curling	
Acanthaster planci	Beach *et al.* 1975	Spawning conspecifics	Laboratory observations: orientation and movement towards conspecifics
Id.	Hanscombe *et al.* 1976	From coral mucus an acidic protein (molecular weight 200,000) induces feeding and low molecular weight inducers are not just mucoprotein components. They postulate that the large molecules could be good antigens, thus food recognition would be related to the 'immune system of higher organisms'	Laboratory observations: orientation and movement towards stimuli
Id.	Huxley 1976	Small molecules can be attractive but for stomach eversion large molecules are necessary. Fresh extracts are more stimulating than old extracts	Laboratory observations: used plaster tablets impregnated with extract
Id.	Moore & Huxley 1976	Aboral arm curling and tube-foot withdrawal could be elicited by whole coral extracts, single amino-acids and their mixtures and nematocyst homogenates	Laboratory observations
Crossaster papposus	Regnart 1928	Mussel tissue	Laboratory observations: orientated towards bait
Id.	Sloan 1977	Live *Crepidula, Asterias* and *Crossaster*	Laboratory observations: orientated to live prey species, but not conspecifics in a Y-maze
Echinaster echinophorus	Ferguson 1969b	Cardiac stomach is readily everted to many soluble nutrients. Amino-acids and sugars such as glucose effectively stimulate ciliary pumping in Tiedemann's pouches	Laboratory observations
Patiria miniata	Araki 1965	The large molecular weight protein albumin is taken up by the everted stomach. Individual amino-acids and carbohydrates are only weakly stimulatory. In summation, stomach eversion is induced by albumin, gelatin, bactopeptone, casein hydrolysate and weakly by individual amino-acids	Laboratory observations: induced stomach eversion

Table 2 (continued)

Species	References	Nature of chemical stimuli	Notes
Patiria miniata	MacGinitie & MacGinitie 1968	*Haliotis* tissue	Laboratory observations: positive orientation and locomotion
Id.	Wobber 1975	Fresh squid tissue	Field observations: aggregation about the bait
Pteraster tesselatus	Mauzey *et al.* 1968	Live sponge	Laboratory observations: located sponge in aquarium 'remarkably' quickly
Asterias forbesi	Nelson 1946	Oyster beds	Field observations: migrate onto oyster beds
Id.	Burkenroad 1946	Oyster beds	Field observations: migrate onto oyster beds
Id.	Anderson 1953	Stomach eversion elicited by acetylcholine, adrenaline chloride would cause retraction and closure of the stomach – see *Acanthaster planci*	Laboratory observations
Id.	Brauer *et al.* 1970	Bivalve extracts	Laboratory observations: stimulated stomach eversion
Id.	Zafiriou *et al.* 1972	Live oysters, oyster tissue and extracts of four bivalves	Laboratory observations: attracted to bivalve homogenates, compare with negative results of Castilla (1972b) and Castilla & Crisp (1970)
Id.	Heeb 1973	Whole and fractions of bivalve extract. High molecular weight (>10,000) clam protein extracts at dilutions as low as 3.4 x 10^{-6} gm/ml could attract the asteroids. No observations on low molecular weight compounds made	Laboratory and field observations: stimulated humping and stomach eversion in the laboratory and *in situ* in the field
Asterias rubens	Romanes 1883, 1885	Fresh crab and mussel meat	Laboratory observations: led the asteroids around with a piece of meat
Id.	Milligan 1915a,b,c	Dead pipe fish	Laboratory observations: dead fish quickly located in aquaria
Id.	Regnart 1928	Mussel meat	Laboratory observations: tissue located in a labirynth maze
Id.	Bull 1934	Live mussels and mussel meat	Laboratory observations: bait quickly located in aquaria
Id.	Henschel 1936 (in: Carthy 1958)	Amino-acids and peptones, but not carbohydrates evoke feeding behaviour	Laboratory observations
Id.	Feder & Christensen 1966	Mollusc meat	Laboratory observations
Id.	Nicol 1967	Strongly attracted to glycogen	No comment given
Id.	Castilla & Crisp 1970	Live mussels and barnacles, crushed bivalves, live *Crossaster*	Laboratory observations: attractive to whole mussels, avoids damaged and spawning mussels and *Crossaster*

Table 2 (continued)

Species	References	Nature of chemical stimuli	Notes
Asterias rubens	Castilla 1972a	Live mussels and oyster spat	Laboratory observations: only attracted to mussels not the oyster spat
Id.	Castilla 1972b	Solutions containing L-glutamic acid, bacterial peptone and individual and mixtures of ten amino-acids were 'repellents'. Sensitive to 7.5 x 10^{-7} g/ml L-glutamic acid. Note: Whittle & Blumer (1970a,b) and Zafiriou *et al.* (1972) found that *A. rubens* is attracted to amino-acids and their mixtures	Laboratory observations: repelled by the extract and peptone. Many other species are attracted to crushed and homogenated prey, e.g. *Luidia, Pisaster, Acanthaster*
Id.	Eriksson *et al.* 1975	Mussel tissue	Laboratory observations: will approach food in a flowing tank
Id.	Anger *et al.* 1977	Buried bivalves (*Macoma*)	Field observations: suggested location of prey requires olfaction
Asterias vulgaris	Smith 1940	Oyster beds	Field observations: would migrate towards prey
Id.	Brauer *et al.* 1970	Extracts of bivalves *Venus* and *Crossastrea* and the active elements are of low molecular weight, heat stable and water soluble	Laboratory observations: stimulated stomach
Id.	Whittle & Blumer 1970a	Live oysters, whole and fractions of oyster extracts. Attracted to stable low molecular weight compounds, (exact nature unknown), polar, low molecular weight organic compounds (2-3 x 10^{-2}) probably amino-acids. Unlike Nicol (1967), glycogen not attractive	Laboratory observations: responded positively to oysters more strongly than three other bivalve species
Id.	Whittle & Blumer 1970b		
Id.	Zafiriou 1972	Various chemicals excluding amino-acids. Response variable but single amino-acids and their mixtures were 'weakly attractive' as were urea, lactic and succinic acid and 'hand sweat'. However, useful to note that non-chemical factors may also affect susceptibility to 'attractive' chemicals	Laboratory observations: responds to a wide range of chemical stimuli but response is variable
Id.	Zafiriou *et al.* 1972	Live oysters, oyster meat and extracts of four other molluscs were attractive. Extracts diluted by 10^{-8} were attractive	Laboratory observations: unlike Castilla & Crisp (1970) and Castilla (1972b) asteroids would approach damaged prey

Table 2 (continued)

Species	References	Nature of chemical stimuli	Notes
Astrometis sertulifera	Jennings 1907	Live crabs and fresh crab meat	Laboratory observations: more sensitive to injured prey than live prey. Jennings called this species *Asterias forreri*
Evasterias troscheli	Christensen 1957	Live *Mytilus*	Field observations: will approach from a distance
Heliaster kubinji	Reese 1966	*Mytilus* extract	Laboratory observations: evokes a 'jerky lunging form of locomotion' with the distal portions of the leading arms raised off the substrate
Marthasterias glacialis	Preyer 1887	Fresh crab meat	Laboratory observations: would approach bait
Id.	Prouho 1890	Live and dead fish	Laboratory observations: would approach bait
Id.	Valentinčič 1973	Extract soaked cotton balls	Laboratory observations: would approach and injest the cotton balls
Id.	Valentinčič 1975	Amino-acids, beef extract, reduced glutathione and glucose are stimulatory. L-cysteine hydrochloride and L-proline were the most stimulatory	Laboratory observations: would approach extract soaked cotton balls
Id.	Valentinčič 1978	L-cysteine	Laboratory observations: this 'stimulatory chemical' elicited searching behaviour or the appetitive phase of the feeding response
Pisaster brevispinus	Smith 1961	Living bivalves	Laboratory observations: would locate and capture buried clams
Id.	Van Veldhuizen & Phillips 1978	Crushed *Mytilus*	Laboratory observations: elicited tube-foot extension down artificial burrow
Pisaster giganteus	Feder & Christensen 1966	Damaged *Haliotis*	Field observations: approaches crushed abalones (C. Linbaugh, personal communication)
	Landenberger 1966, 1968	Live *Mytilus*	Field observations: aggregation in areas of high mussel density
Pisaster ochraceus	Landenberger 1968	Live *Mytilus*	Field observations: aggregation in high density mussel areas
Id.	MacGinitie & MacGinitie 1968	Crushed *Mytilus*	Will approach crushed mussels
Pycnopodia helianthoides	Wobber 1975	Actively feeding asteroids	Field observations: was seen to approach *Pisaster* while it was feeding on mussels
2b. Negative reports of asteroid distance chemoreception			
Luidia sp.	Preyer 1887	Fresh crab meat	Laboratory observations: could not demonstrate olfaction, suggested possible satiation of test individuals

Table 2 (continued)

Species	References	Nature of chemical stimuli	Notes
Astropecten bispinosus	Preyer 1887	Fresh crab meat	Laboratory observations: could not demonstrate olfaction, suggested possible satiation of test animals
Astropecten spp.	Doi 1976	Live prey species	Field observations: hunts by 'crawling on the sand surface and recognising them by bodily contact', no mention of olfaction
Asterina gibbosa	Kalmus 1929	Crushed bivalves	Laboratory observations: no definite orientation to the food was demonstrated (in: Feder & Christensen 1966)
Crossaster papposus	Bull 1934	Live oysters	Laboratory observations: orientation to distant food could not be demonstrated
Id.	Mauzey *et al.* 1968	Live nudibranchs	Laboratory observations: orientation to distant food could not be demonstrated
Id.	Hancock 1974	Live mussels and oysters	Laboratory observations: orientation to distant food could not be demonstrated
Pteraster tesselatus	Rodenhouse & Guberlet 1946	Scallop extract	Laboratory observations: 'refused extract' but they did not specify active avoidance or merely no reaction
Solaster dawsoni	Mauzey *et al.* 1968	Five species of prey asteroids	Field observations: even at close proximity, no indication of prey being sensed
Solaster endeca	Bull 1934	Live *A.rubens*	Laboratory observations: concluded no olfactory ability
Asterias forbesi	Galtsoff & Loosanoff 1939	Live oyster	Laboratory observations: asteroids not attracted to prey in a large outdoor tank
Id.	Loosanoff & Shipley 1947	Cages with nine different baits	Field observations: could not demonstrate strong orientation to the bait
Asterias vulgaris	Dickie & Medcof 1963	Live scallops	Laboratory observations: could not locate prey directly
Leptasterias hexactis	Menge 1972	Living 'prey' species	Laboratory observations: after 49 Y-maze tests no consistent choice for food recorded, quantitative data not provided
Meyenaster gelatinosus	Dayton *et al.* 1977	Numerous living prey species	Field observations: suggested that asteroids generally have poor distance perception

reception for each species are listed in table 2. Casual field and laboratory observations as well as controlled laboratory experiments, when combined, provide both positive (73 %), negative (22 %), and inconclusive (5 %) evidence for asteroid olfaction (table 2a, b). The negative results (table 2b) must therefore be regarded as significant. Of these negative reports, however, only two concern experiments with chemical extracts or enhanced availability of stimulant such as is caused by crushing. This, together with the considerable experimental work on the subject indicate that most predatory asteroids have an olfactory ability.

Field work on asteroid and indeed all echinoderm olfaction is minimal, probably because of the difficulty of finding suitable experimental sites and the relatively recent innovations of SCUBA. Ormond *et al.* (1973) and Ormond & Campbell (1974) used Y-maze choice chambers *in situ* to examine olfaction in *Acanthaster planci* in the Red Sea. In these conditions results are difficult to evaluate on account of unknown water currents and olfactory stimuli from outside the experimental area. Nonetheless their approach to eliminating experimental artifact, induced in animals by captivity and handling in the laboratory, ought to be repeated in other echinoderms. It would be most valuable to get more *in situ* verification of chemoreception in other echinoderm species.

In the century or so that has elapsed since the demonstration by Romanes (1883) of leading an asteroid around with a piece of meat just in front of it, experimental approach has refined greatly. Many of the asteroid olfaction reports were completed with living, crushed or crude whole extract of prey and employed simple methods for monitoring behaviour. To improve the choice criteria, many workers have used mazes, known as olfactometers. These allow animals to orient to 'bait', often with the potential for an alternative. Other chemically mediated behavioural criteria used have been stomach eversion preparatory to feeding (Anderson 1953, Araki 1965, Brauer *et al.* 1970, Heeb 1973), distal arm tips and terminal tube-foot responses (Moore & Huxley 1976), and increased ciliary pumping activity in the Tiedemann's pouches (Ferguson 1969b).

The most significant laboratory work has been carried out with the use of olfactometers. The most popular olfactometer for use in the laboratory is the flowing Y-maze pioneered by Davenport (1950). It provides a critical choice situation at the arm junction in which two entirely different water bodies can become confluent in a non-turbulent fashion. Thus discrete water borne chemicals are presented for a test organism to choose between, and it also has what Ache & Davenport (1972) have described as 'binomial simplicity' because the results it provides are amenable to statistical analysis.

Several points arise in appraising olfactometer work from the original papers: were freshly collected animals used; were the storage and maintenance conditions experienced by the animals appropriate; were seasonal changes in the test animal considered; what potential contamination could be important to the test water? Considering the test animals' responses, what of innate behavioural variability of echinoderms (Zafiriou 1972, Sloan 1977), which is mentioned in detail later, or the difference between a positive olfactory response or a rheotactic one (Castilla & Crisp 1973)? Although most olfaction experiments do not include consideration of all the above points, they nonetheless have demonstrated olfaction. There should be more studies like the extensive ones of Castilla (1971, 1972a, b) and Castilla & Crisp (1970, 1973) on *Asterias rubens* with more detail on the animals as behavioural units and not just as quantitative ones in a statistical study.

Analyses of chemicals stimulatory in olfaction and their controlled application to test animals has improved the sensitivity and value of experimental work. Table 2 contains some information on the stimulating chemical compounds. Heeb (1973) divided research effort in this field into three phases. The first consists of descriptive accounts of chemically mediated feeding behaviour before 1955. This phase is being continually augmented, for example, the numerous recent casual observations listed in table 2. His second phase began with the discovery in 1955 of a small molecular weight compound, glutathione, which specifically releases feeding behaviour of *Hydra.* Since then work on food chemoreception in coelenterates has advanced rapidly (Lenhoff & Lindstedt 1974, Lenhoff 1974, 1975). In all echinoderms, however, work of this nature is just beginning. For example, Zafiriou (1972), Valentinčič (1973, 1975) and Moore & Huxley (1976) have all shown that amino acids and other low molecular weight compounds attract asteroids (for details of the compounds, see table 2). In most cases mixture of these amino acids act synergistically to enhance the response of asteroids as has been reported in other invertebrates as well (Mackie 1973). Heeb's (1973) third and final phase began in 1971 with publications demonstrating that high molecular weight compounds like proteins stimulated feeding behaviour in polychaetes. In fact Araki (1965) had already shown that the protein albumin stimulated feeding in *Patiria miniata.* Mackie (1975) noted the 'extreme importance' to slow moving animals like asteroids of the different diffusion coefficient of macromolecules and low molecular weight amino acids. He stated that 'in the absence of water currents, any signal composed of amino acids will be relatively short lived'. Heeb (1973) reported that a protein extracted from clams attracted *Asterias forbesi* while Hanscombe *et al.* (1976) stated that a mucoprotein from coral prey attracts *Acanthaster planci.* Other recent work on *A.planci* has shown that both high and low molecular weight compounds, the latter not necessarily being components of the former, may have different roles in activating feeding (Collins 1975a, Huxley 1976). This is most interesting and there should be further work on the separate roles of proteins and amino acids now that both some high and a wide range of low molecular weight molecules are known to be stimulatory in asteroid olfaction. More effort in this field should go to other echinoderm classes which present great opportunities for researchers.

3.2. *Ophiuroids*

Hyman (1955 pp.661-662) reviewed olfaction in ophiuroids and cited the early confirmation by Des Artes, Preyer and Von Uexküll of olfaction in *Amphiura, Ophiomyxa* and *Ophiura.* Other accounts of both olfaction and gustation in ophiuroids are listed in table 3. Since ophiuroids are generally polyphagous feeders (Fontaine 1965, Chartock 1972, Wilson *et al.* 1977) which augment suspension feeding with opportunistic scavenging and predation, it is not surprising that so many genera are chemoreceptive to food.

By comparison with asteroids, ophiuroids present certain innate difficulties. Generally they are smaller and more fragile and some aspects of their anatomy (e.g. the skeleton) have hindered anatomical and physiological investigations. On the other hand, they are abundant, active and readily respond to a wide range of stimuli. In the light of exciting recent neurophysiological advances (Brehm 1977, Brehm & Morin 1977) on *Ophiopsila californica,* these may be the best suited echinoderms for investigating the neurosensory basis of echinoderm chemoreception. Ophiuroids have relatively large diameter axons in their radial cords which are more amenable to intracellular recording. Thus action potentials could be monitored after the administration of chemical stimuli. Besides demonstrating the physiological evidence for chemoreception, this would also be a useful and defini-

Table 3. Ophiuroid chemoreception

Species	References	Nature of chemical stimuli	Notes
Amphipholis (= Axiognathus) squamata	Martin 1968	Mussel (*Mytilus*) tissue, meat extract, carmine particles	No response to meat but suggested that arm podia could have 'gustatory powers'
Ophiactis resiliens	Pentreath 1970	Large suspended food particles	Gustation in arm podia is possible
Ophiothrix fragilis	Nagabhushanam & Colman 1959	Mixed fish bait in a crab trap	Attracted to the bait
Ophiocoma anaglyptica	Chartock 1972	Fish (*Acanthurus*) tissue	Responded when tissue was introduced into an aquarium
Ophiocoma dentata	Chartock 1972	*Enteromorpha* and *Acanthurus* tissues	Orientated to these potential foods from 5-10 cm away
Ophiocoma doederleini	Chartock 1972	*Enteromorpha* and *Acanthurus* tissues	Claimed 'Chemosensory detection' of these tissues
Id.	Sloan (unpublished)	Fish tissue	Increased activity and orientation towards tissue
Ophiocoma erinaceus	Sloan (unpublished)	Fish tissue	Increased activity and orientation towards tissue
Ophiocoma scolopendrina	Magnus 1967	Mollusc and algal extracts	'Winding' arm response to the extracts, gustatory ability in the podia
Ophiocoma riisei (= *O. wendti*)	Cowles 1910	Fish tissue extract-soaked paper boluses plus tissue fragments themselves	Some gustatory powers present in the tube-feet but no mention of olfaction
Ophiocomina nigra	Nagabhushanam & Colman 1959	Mixed fish bait in a crab trap	Attracted to the bait.
Id.	Fontaine 1965	Chopped mussel (*Mytilus*) and herring (*Clupea*)	Orientation to this tissue and he suggests that distance chemo-receptors in the buccal tube-feet while weak contact chemoreceptors in arm tube-feet
Id.	Wilson *et al.* 1977	Scallop (*Chlamys*) extract	Increased activity and orientation to food source. Attacks only damaged *Ophiothrix* which may release body fluids
Ophiopteris antipodum	Pentreath 1970		Gustatory ability of buccal tube-feet
Ophionereis fasciata	Pentreath 1970	Mucus-food boluses	Only buccal tube-feet implicated in gustatory quality assessment of food boluses
Ophioderma appressum *Ophioderma brevicaudum* *Ophioderma cinereum* *Ophioderma rubicundum*	Reimer & Reimer 1975	23 amino-acids reduced glutathione, niacine, plus crab, fish, and echinoid viscera extract	All species activated by glycine and niacine; 3 by ornithine and hydroxy-proline; 2 by leucine and isoleucine and 1 by proline. Responses to animal extracts were similar to the strongest responses evoked by the chemicals
Ophioderma longicauda	Deschuyteneer & Jangoux 1978	(1) Mussel and fish meat (2) Fish blood, glycine, nicotinamide	Not attracted to rotting carrion or to (2); attracted to (1) especially after 8-10 days starvation
Pectinura maculata	Pentreath 1970	Mussel (*Mytilus*) tissue	Readily detected and grasped by tube-feet

tive bioassay for testing the potential for particular chemicals to be stimulatory. The partnership of neurophysiology and chemoreception in molluscs (Jahan-Parwar 1972, Stephens 1978), for example, has been most productive.

On the whole animal level, more experimentation is needed as most of the references to ophiuroids are anecdotal (table 3). Controlled studies using olfactometers should be done. In the only study on the chemicals stimulatory to ophiuroids, Reimer & Reimer (1975) listed some of the amino acids like proline and leucine that also stimulate asteroids (table 3). A comparative study of the chemicals that stimulate asteroids and ophiuroids could prove very interesting. Of all the echinoderm classes ophiuroids have the greatest potential in future chemoreception research.

3.3. *Echinoids*

In contrast to ophiuroids, echinoids have attracted more workers and a good deal is known about their feeding biology although their sluggish responses to chemical stimuli have rendered them poorly worked in this latter field. Lawrence (1975a) published a comprehensive review of the relationships between marine plants and echinoids which considered food perception. Since that date, with a few exceptions, little else on echinoid chemoreception has appeared. It should be noted that throughout the work on echinoids there has been a strong bias towards plant food. Plant food preferences, which are probably linked to chemical characteristics and nutritional value of the food, are well-known in echinoids (Lawrence 1975a:231) and play an important role in their ecology (Vadas 1977, Ott & Maurer 1977). Vadas (1977) has indicated, however, that in nature a compromise between food preference and availability occurs. Regular echinoids have long been regarded as significant herbivores in marine habitats, but in reality many species especially cidaroids are omnivorous if not carnivorous (McPherson 1968, Sammarco *et al.* 1974, Bak & Van Eys 1975, Karlson 1978). Further investigation of the perception of animal prey by echinoids is needed.

There are a number of reports of field investigations on echinoid food perception. Observations on the genus *Strongylocentrotus* have dominated the field. Leighton (1971), Himmelman & Steel (1971) and Garnick (1978) showed that this genus is attracted towards algae. Larsson (1968) using *Psammechinus miliaris* also noted attraction to drift algae. Himmelman & Steel (1971) removed echinoids from an algal food-rich area and observed their return. Similar results were obtained by Leighton (1966), Fuji & Kawamura (1970), North (1971), Mattison *et al.* (1977) and Garnick (1978) with *Strongylocentrotus* species. They showed this genus to be attracted to algal stands and kelp beds. Some workers have endeavoured to relate perceptive behaviour with the abundance of available food. North (1971) noted that there was more foraging with lower concentrations of algae.

It should be pointed out that techniques available, such as the use of exclusion cages, could be of great advantage when employed primarily to establish field data for echinoids themselves. It seems desirable for a wider selection of genera for investigations.

There have been several reports of qualitative evidence for chemical perception of food based on laboratory observations. Milligan (1916), Lewis (1958), Leighton (1971), and Garnick (1978) have shown that the presence of food stimulates increased tube-foot activity, directional and masticatory movements of echinoids. Several workers have attempted to stimulate echinoids with algal extracts (Sammarco 1972a, in Lawrence 1975a, Vadas 1977). Leighton (1971) showed that *Strongylocentrotus purpuratus* was attracted to an extract of the giant kelp *Macrocystis.* Unfortunately, very little has been done on the precise characterisation of the chemicals stimulatory to echinoids. This is a wide open field in which knowledge of the chemical stimulants derived from algal food would be particularly useful. Leighton (1971) found that the 'scent' of *Macrocystis* was attractive to *S. purpuratus* but not to *Lytechninus anamesus.* Garnick (1978) reported that *Strongylocentrotus droebachiensis* was sensitive to distant food and to conspecifics as well.

Echinoids have proved relatively favourable for experimental work and are easier to maintain in captivity than other echinoderms. Their suitability for laboratory experimentation in the realms of perception has yet to be exploited. Campbell & Laverack (1968) noted that globiferous (gemmiform) pedicellariae respond to algal extracts and lobster haemolymph. Clearly chemoreceptors are widely distributed on the echinoid test and among its appendages and these are freely available for investigation (Campbell 1976). The role of the sensory hillock of globiferous pedicellariae will be discussed later in this review. Little analytical work has been done on echinoids using extracts and food related chemicals such as amino acids.

Irregular echinoids have not been investigated. Since most are infaunal, contact chemoreception of the substrate may be more important than olfaction but this is speculation. The whole issue of substrate selection and substrate/food perception in irregular echinoids warrants attention.

3.4. *Holothuroids*

Hyman (1955) considered the chemosensitivity experiments reported in early holothuroid papers (Pearse 1908, Crozier 1914, 1915, Olmstead 1917, Yamanouchi 1929) 'must be regarded rather as an exercise in physical chemistry than as related to the life of animals in nature'. Other early papers are anecdotal like H.L.Clark (1909) who reported that *Synapta* (= *Leptosynapta*) *inhaerens* would avoid a decaying asteroid or Tao (1930) who stated that *Caudina chilensis* would react to chemical stimuli without describing the stimuli. Glynn (1965) reported that *Leptosynapta albicans* and *Astichopus multifidus* would respond to extracts of potential predators. Berrill (1966) found that another tropical species *Opheodesoma spectabilis* did not react to extracts of crustaceans or *Sargassum* but apparently recognised *Sargassum* upon contact. Fankboner (1978) reported that tentacle tips of *Psolus chitonoides* responded to 'stale' seawater and suggested that this was a chemosensory response. The idea of an olfactory ability in holothuroids was supported by Nicol (1967, p. 350) although he cited no references. Bakus (1973) on the other hand assumed that tropical species possessed poor chemosensitivity citing, as an example, the numerous reports of individuals ingesting their own feces. Massin (1980b) found that holothuroid feces contain more organic matter than ambient sediments. The belief that this is a widespread phenomenon among deposit feeders is, however, now in question (Levinton *et al.* 1977).

Some recent work on holothuroids has demonstrated that they are selective of sediment particle size and, in most cases, larger animals ingest larger particles (Rhoads & Young 1971, Bakus 1973, Hansen 1978, Roberts 1979, Sloan 1979). Holothuroids are believed to utilise micro-organisms associated with particles (detritus) rather than the detritus itself (Bakus 1973, Yingst 1976). Massin & Jangoux (1976), however, could not demonstrate body size-related particle size selection in *Holothuria tubulosa* and *Holothuria poli.* Similarly, Moriarty (1978) reported that particle size selection did not occur in *Holothuria atra* and *Stichopus chloronotus* although he suggested 'some mechanism for selecting particles rich in bacteria'. Massin & Jangoux (1976) proposed that contact-chemosensitivity was used by *H.tubulosa* when selecting sediments rich in organic material although they provided no quantitative data. Webb *et al.* (1977) also suggested that *H. atra* selectively ingests sediments rich in organic carbon. Webb *et al.* (1977), Moriarty (1978) and Massin (1980b) demonstrated greater concentrations of organic matter or bacterial biomass in the holothuroid's guts than the ambient sediments. Further work must be done on this because the selection mechanism of sediment quality by holothuroids is still poorly understood. Roberts (1979) has shown that particle size selection may be related to the surface structure of holothurian tentacles. Knowledge on stimuli that evoke holothuroid feeding is an important field because holothuroids are such important sediment reworkers in shallow waters (see Massin, chapter 23).

The apodids, being the most active holothuroids and thus the most amenable to behavioural bioassay, have received most attention. Definitive work on chemoreception and the physiology of their chemoreception senses in holothuroids is lacking. There should be detailed chemoreception studies on deposit feeding and suspension feeding holothuroid species and a comparison between a semi-sedentary deposit-feeder (e.g. *Holothuria*) and a mobile deposit-feeder (e.g. *Synapta*). Until such work is done, holothuroid chemosensivity will remain a speculative topic.

3.5. *Crinoids*

Hyman (1955) cited the only two references on crinoid chemoreception. In 1884 Marshall reported that *Antedon mediterranea* was insensitive to chemical stimulation on its aboral side. Gislén (1924) used carmine particles treated with crab hepatopancreas to activate tube feet, pinnules, and arms of *Antedon petasus.* No satisfactory chemoreception studies have been reported on crinoids in the last 50 years. Clearly the role, if any, of chemoreception in all suspension feeding crinoids needs investigation.

4. ORGANS OF CHEMORECEPTION

Although echinoderms are well-known to be sensitive to chemical stimuli, very little information is available on their methods of chemoreception and we know of no current work in this field. An overall chemosensitivity to a wide range of stimuli has been suggested by Hyman (1955). Pentreath & Cobb (1972) have proposed that unspecialised epithelial sensory cells are receptive to light, mechanical and chemical stimuli.

Early references to echinoderm chemosensory organs are generally anecdotal and no definitive work in this field has been done. Hyman (1955:63) stated that crinoids are poorly endowed with sense organs with the exception of papillae on the tube feet. She figured these from an early illustration by Hamann (1889), whose work was then the most extensive source of histological description of tentative echinoderm sensory sites. Gislén (1924) implied chemoreception in *Antedon petasus* while Hyman cited the rapid responses of arms, pinnules and tube-feet to crab hepatopancreas extract. Perhaps the whole surface is chemosensitive.

Hyman (1955:611) stated that 'ophiuroids are devoid of special sense organs' although she indicated the 'rich innervation of body wall, podia, and spines' and later (p.662) she stated that 'food perception is probably located in the podia'. The tube-feet of at least 10 species have been credited with either olfactory or gustatory abilities by Cowles (1910), Fontaine (1965), Magnus (1967), Martin (1968) and Pentreath (1970). In the only specific study of chemoreception in ophiuroids Reimer & Reimer (1975) state no opinion as to ophiuroid chemoreception sites.

No specific sites on asteroids have been confirmed as chemosensory areas although Sloan (1980a) has reviewed the implication of the distal arm area, which includes the delicate terminal or sensory tube-feet, as potential chemosensory areas. Studies on *Acanthaster planci* (Brauer *et al.* 1971, Moore & Huxley 1976), *Marthasterias glacialis* (Valentinčič 1973, 1975) and *Crossaster papposus* (Sloan 1980a) describe chemically mediated responses in this area. It has been shown that physical, photic and chemical stimuli evoke the same sensory tube foot movements and arm tip curling responses (Sloan 1980a). As the leading portions of the mobile animal these areas are most likely to encounter and perhaps monitor changes in the animal's sensory milieu. Sloan (1980a) suggested that the evolution of the terminal arm area into particularly sensory areas could have arisen from the use of the upturned arm tips in primitive obligate infaunal asteroids, like *Ctenodiscus crispatus,* for access to water and thus respiratory current generation. Facultative burrowers like *Luidia* and *Astropecten* have exposed arm tips with active sensory tube-feet when buried yet they readily emerge when chemically stimulated (Fenchel 1965, Christensen 1970). Histological and physiological evidence of asteroid chemoreception, however, is greatly needed and examination of the sensory tube-feet is needed especially.

Ayres (1886) suggested that echinoid sphaeridia were chemosensory after observing their reactions to acetic and chromic acids; highly artificial stimuli but fashionable at that time! Although not necessarily feeding related, the only structures fully examined and described as echinoderm chemoreceptors are the 'sensory hillocks' in the inside of the valves of globiferous pedicellariae of *Echinus esculentus* (Campbell & Laverack 1968, Laverack 1968b). Cobb (1968b) described its structure, which consists of about 2,000 epithelial cells. The surface of each cell has a cilium surrounded by a ring of microvilli. Cobb (1968b) also demonstrated an axonal connection of the hillock with the neuropile at the base of the jaws. Later Chia (1969f) confirmed that chemical stimulation was important to the action of sensory hillocks in globiferous pedicellariae of other echinoids besides *Echinus.* Chia (1970) believed that the globiferous pedicellariae of *Psammechinus miliaris* are more chemosensitive than those of *Echinus esculentus* and *Strongylocentrotus droebachiensis.* Norrevang & Wingstrand (1970) describe choanocyte-like cells in the coelomic tissues of *Asterias rubens, Porania pulvillus* and *Stichopus regalis,* very similar to the ones described by Cobb (1968b). Norrevang & Wingstrand (1970) suggested that it is a fundamental cell type in metazoans. They believed that the works of Campbell (in Laverack 1968b) and Cobb (1968b) also described modified choanocyte-like cells which, now sensory, originated from phagocytic cells of the cutaneous epithelium. There is a noteworthy parallel between these cells and the pinocytotic cells mentioned in Lenhoff's (1975) hypothesis of the origin of cellular receptor sites. He proposed that coelenterate pinocytotic cells which take up nutrients also respond to a broad range of chemicals, and cited as evidence the rapid formation of a microvilli network at the apical end of endodermal digestive cells in the gut of *Hydra* stimulated by certain amino acids. Lenhoff (1975) suggested an evolutionary sequence from receptor sites on single cells inducing pinocytosis to co-ordinated feeding responses in simple animals like coelenterates and the receptor sites for neurotransmitters and hormones of higher organisms. O'Connell *et al.* (1974) provided further histological descriptions of the internal surface sensory epithelium of the jaws of globiferous pedicellariae although they did not assign any particular sensory function to it. Oldfield (1975) reported a detailed study of the surface fine structure with the SEM. Campbell (1976) demonstrated the chemosensitivity of echinoid globiferous pedicellariae, thus confirming the sensory hillock as the first definite echinoderm chemoreceptor. It should also be mentioned that Hamann (1887, plates 2 and 3) illustrated similar structures from *Sphaerechinus granularis, Echinus esculentus* and *Paracentrotus lividus* which Hyman (1955) called 'tangoreceptors' (mechanoreceptors). Lawrence (1975a:236) reviewed what little has been observed of echinoid tube-feet responding to chemical stimuli starting with Milligan's (1916) observations of *Psammechinus miliaris* tube-feet waving in response to distant food.

Among the holothuroids, apodids are considered to have the most complicated sense organs (Hyman 1955). Sensory sites on the inner surface of apodid tentacles are considered potentially chemosensory (Hyman 1955), indeed, H.L. Clark (1909) called them olfactory 'cups' in *Synapta inhaerens.* Fankboner (1968) suggested that warty papillary cells on the tentacle tips of the dendrochirote *Psolus chitinoides* may be chemosensory.

As with the problems with electrophysiology of the echinoderm nervous systems, advances in techniques may be necessary before the interesting and important field of echinoderm chemoreceptors can advance. However, if there is an overall chemosensitivity ability in echinoderms, would specific chemoreceptor sites be necessary?

5. VARIABILITY OF RESPONSE TO CHEMICAL STIMULI

In his study of the response of *Asterias vulgaris* to chemical stimuli, Zafiriou (1972) encountered considerable variability in the behaviour of his test animals. He concluded that 'the anticipation of stereotyped behaviour may have led to the confused state of asteroid feeding behaviour literature'. As has previously been indicated there have been conflicting reports as to olfaction in the asteroids. Although the other classes are poorly covered in the literature in this respect, probably considerable behavioural variability occurs in echinoderms generally.

Early workers on ophiuroids (Glaser 1907) and asteroids (Romanes & Ewart 1881, Jennings 1907) mentioned variability of different individuals to uniform stimuli. Bohn (1908) and Jennings (1907) suggested that the internal physiological state of the asteroids could be responsible. Variability in asterozoan escape and righting behavior was related by Reese (1966) to their radial symmetry in that they 'face the environment from all sides' and thus can respond in many different ways. Some variability in asterozoan feeding responses, which could be considered response to chemical stimuli, can be under a season-temperature influence (Mauzey *et al.* 1968, Mackenzie 1970b, Castilla 1972a, b); captivity, handling and starvation influence (Landenberger 1968, Mauzey *et al.* 1968, Castilla & Crisp 1973, Reimer & Reimer 1975); innate differences between individuals (Collins 1974, 1975a, b); and ingestive conditioning (Landenberger 1966, 1968, Castilla & Crisp 1970, Castilla 1972a, b, Zafiriou 1972, Zafiriou *et al.* 1972, Collins 1974, 1975a, b, Huxley 1976, Ormond *et al.* 1976). 'Ingestive conditioning' (Wood 1968) is a process in which an animal's food preference is influenced by recent feeding experience which usually manifests itself in a positive reinforcing way. This could be interpreted as learning. Both associative learning and habituation abilities based almost entirely on asteroid work have been attributed to echinoderms (Reese 1966). There are more recent reviews of echinoderm learning (Binyon 1972a, Willows & Corning 1975) but Reese (1966) had studied the literature the most deeply.

Since Reese (1966), little work on echinoderm learning has been done, but Valentinčič (1978) demonstrated associative learning in the avoidance by *Marthasterias glacialis* of attractive food models combined with unattractive electrical shocks. He considered that feeding and avoidance behaviour of *M.glacialis* as 'flexible behavioural patterns which may be triggered by convenient stimuli'.

The innate variability of echinoderms is poorly understood but it is clear that uniformity of responses to similar stimuli is not an echinoderm characteristic. Numerous authors like Mauzey *et al.* (1968) stress that the feeding of captive echinoderms should not necessarily be depended upon as an accurate portrayal of feeding habits in nature. Perhaps the answer is detailed long term observations of undisturbed animals *in situ.*

6. CONCLUSIONS

It seems certain that many echinoderms possess olfactory as well as gustatory abilities. Probably a gradation of olfactory ability exists between the free-living predatory and grazing forms through to the sedentary filter feeding groups and substrate ingestors, where physical discrimination may become relatively important. Because of their relatively undynamic life style and flexible metabolism, echinoderms can survive extended periods of starvation. Warden *et al.* (1940) wrote '. . . time is a relatively unimportant fact in the life of these animals . . . the biologically significant fact is the successful completion of a given act no matter how varied or time consuming the movements are which lead to its accomplishment'.

Chemoreception remains one of the lesser known sensory modalities of echinoderms although it undoubtedly is a vital attribute to many species and there is much room for research in this field.

DAVID L. MEYER

2

FOOD AND FEEDING MECHANISMS: CRINOZOA

1. TROPHIC CLASSIFICATION

Assignment of crinoids to the correct trophic category depends upon a clear understanding of the basic food gathering mechanism. The crinoid feeding mechanism relies on environmentally produced water movements to carry suspended food particles to the extended tube feet which are the primary food capturing organs. With the aid of mucus secretions the tube feet transfer particles to the ambulacral grooves where they are concentrated into strings of mucus which are conveyed to the mouth by ciliary currents. Reliance on water movements means that crinoids must be considered at least moderately rheophilic suspension feeders (Fell 1966a). Classification of crinoids as 'awaiters' (Turpaeva 1957) and as 'fixed net fishers' (Friedrich 1969) carries the implication of rheophilic behaviour. Because of the vigorous activities of the tube feet, Jørgensen (1966) claimed that crinoids are not passive suspension feeders. However, passive suspension feeders are defined as those relying on exogenous currents (Wainwright *et al.* 1976) so that crinoids should properly be placed in this trophic category. Crinoids share this trophic category with other sessile invertebrates such as basket stars, alcyonarians, and corals.

Observations of living comatulid and stalked crinoids in the natural environment (H.L. Clark 1915, Magnus 1963, Rutman & Fishelson 1969, Meyer 1973a, Fishelson 1974, Macurda & Meyer 1974, LaTouche 1978) support the classification of crinoids as passive rheophilic suspension feeders. Several possibilities for alternative trophic roles among living and ancient crinoids must also be considered. Before living crinoids were observed in nature, it was generally supposed that crinoids extended the arms horizontally or with an upward inclination to capture food particles falling by gravitative settling. This behaviour, termed rheophobic by Breimer (1969), now appears to be restricted to deep-water crinoids experiencing periods of slack water (Pérès 1959). Breimer (1969, 1978) has also interpreted several fossil forms having rigid or partly flexible stalks as rheophobic suspension feeders. Although some shallow-water comatulids prefer cryptic or semi-cryptic microhabitats where water movements are very gentle, they are most abundant where there is persistent water movement over the surrounding reef (Meyer 1973a). This suggests that these species also rely on very low velocity flow which circulates through the reef infrastructure. Thus they cannot be considered rheophobic in the strict sense.

While crinoids are generally considered to derive their food supply from particles suspended above the substratum, the utilization of benthic food materials by deposit feeding may be adopted occasionally. Observations from a submersible by Reyss & Soyer (1965) showed that the comatulid *Leptometra phalangium* rests directly on a soft substratum with the oral side upward and the arms held horizontally. They suggested that this may indicate

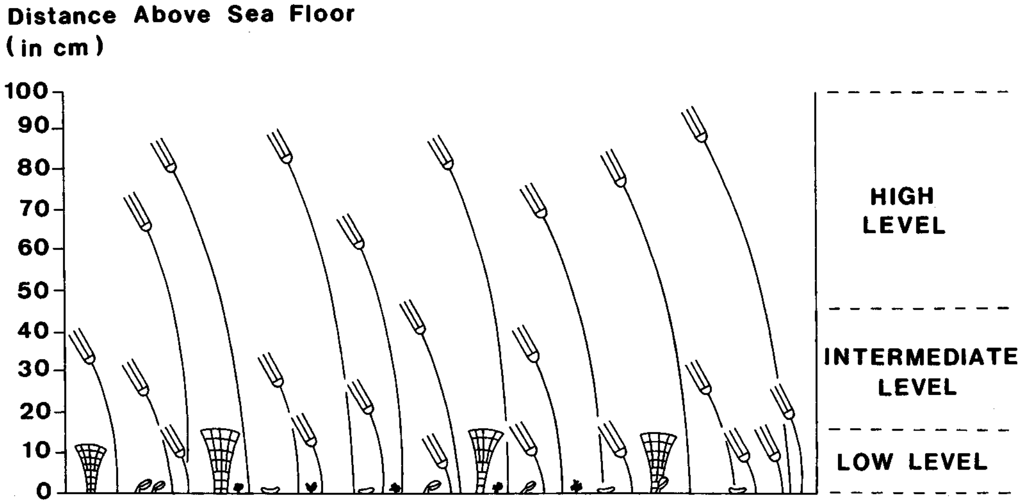


Figure 1. Schematic diagram of stratified community of Middle Paleozoic (Mississippian) crinoids and other epifaunal invertebrates, based on reconstructions of height of living position above sea floor (after Ausich 1980).

deposit feeding habits, although the same species also holds the arms in a vertical filtration fan during periods of current flow. They did not directly observe transfer of benthic particles to the mouth, but the use of the tube-feet for this mode of feeding does not seem unreasonable. In Fiji I have observed the five-armed comatulid *Eudiocrinus* sp. attached by the cirri to the vertical forereef wall, with the arms spread out in contact with the substratum. It is possible that in this situation also the tube-feet may collect particulate food material from the surface of the rock substratum. It is well known that some ophiuroids utilize suspension feeding or deposit feeding depending on the presence or absence of currents (Magnus 1964, Woodley 1975). Deposit feeding has been suggested for certain stemless Paleozoic crinoids that rested directly on the sea floor (Ettensohn 1976, see also Kirk 1911).

In living comatulid crinoids of the family Comasteridae the proximal pinnules are specialized in the possession of teeth on the distal segments which form a terminal comb. The entire pinnule is highly flexible and lashes inward and outward from the oral disk, coiling at the tip. These proximal pinnules appear to function as do the pedicellariae of echinoids to rid the oral surface of foreign particles (Meyer 1973a). However, Gislén (1924) suggested that the comb teeth perform a secondary feeding function by pinching off particles of algae or bryozoans and transferring them to the food grooves. In many hours of observing comasterids *in situ,* I have not seen the comb teeth perform this function. The comb-bearing pinnules are generally not long enough to reach the substratum. However, combs of *Comaster* sp. are present on pinnules far out on the arm. Because some species of this genus cling to the substratum with the arms, it seems possible that these distal comb-bearing pinnules could perform the 'grazing' function suggested by Gislén. Field documentation is required before deposit feeding and grazing can be accepted as alternative modes of feeding in crinoids.

1.1. *Stratification of feeding positions*

The elevation above the bottom at which epifaunal organisms feed has been recognized as an important parameter of trophic classification (Turpaeva 1957, Walker & Bambach 1974). Studies of fossil and living crinoids have demonstrated that crinoids can by no means be lumped within a single category as 'high-level' suspension feeders. In the first place, several groups of ancient crinoids lived a pelagic existence at least during part of their life. These include the Devonian *Scyphocrinites* which was suspended from a terminal float on the stem (Haude 1972), and the gigantic *Seirocrinus* of the Jurassic which is believed to have attached to floating logs (Seilacher *et al.* 1968; although an alternative interpretation was given by Rasmussen 1977). Better known examples are the stemless Cretaceous forms, *Uintacrinus* and *Saccocoma* (see Breimer 1978). Although many Recent comatulids have swimming ability, none are known to be pelagic.

Analysis of stem lengths in species-rich assemblages of mid-Paleozoic stalked crinoids has led to the concept of 'tiered' or 'stratified' epifaunal level-bottom communities of crinoids and other benthos (Lane 1963, 1973, Ausich 1980, Ausich *et al.* 1979). Interspecific differences in adult stem length form the basis for a three-tiered stratification of these crinoid communities (fig.1, Ausich 1980). A different type of stratification has been recognized within Recent communities of reef-dwelling comatulid crinoids. Some comatulids preferentially cling to alcyonarian whips and fans or sponges, providing elevation above the sea floor similar to that of a stalked crinoid. Others gain elevation above the surrounding reef by perching on prominent coral heads or rocks. These comatulids can be regarded as functional stalked crinoids (Meyer & Macurda 1977). Other comatulid species occurring on the same reefs are semi-cryptic, attaching within hidden crevices and extending the arms at levels closer to the floor of the reef and some are totally cryptic in small caves within the reef infrastructure (Meyer 1973a, b).

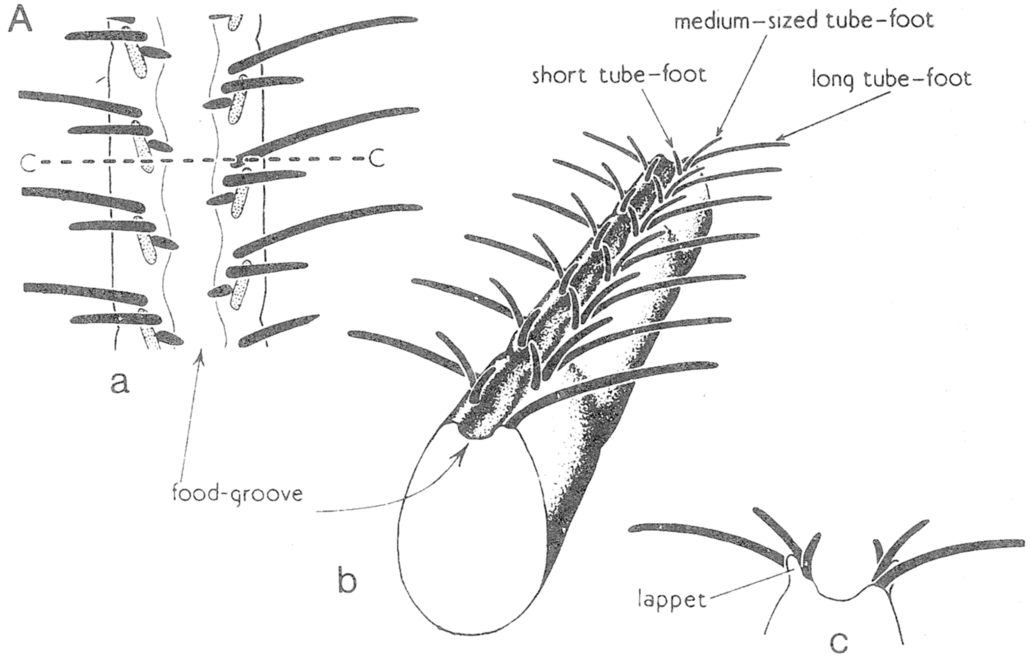
1.2. *Feeding periodicity*

Direct observation of Recent comatulids on coral reefs has revealed that many species are entirely cryptic by day but emerge for feeding by night (Magnus 1963, Meyer 1973b, Rutman & Fishelson 1969, Fishelson 1974, Meyer & Macurda 1980). Species feeding nocturnally occupy elevated as well as semi-cryptic feeding sites, and thus contribute to the complex daily cycle of changing resource utilization on a reef. The ultimate biological significance of this nocturnal behaviour is not yet understood. One possibility is that nocturnal feeders specialize on nocturnally emergent reef plankton. It has also been suggested that disturbance or predation by diurnal fishes has made nocturnal feeding advantageous (Magnus 1963, Meyer & Macurda 1977).

2. FUNCTIONAL MORPHOLOGY OF FEEDING APPENDAGES

2.1. *Tube-feet*

The morphology of the tube-feet of crinoids has been studied in detail in only a few species (Hamann 1889, Reichensperger 1908, Nichols 1960, 1962b, 1966, 1972, Holland 1969). Available information suggests overall similarity in structure and function among all living crinoids, stalked and unstalked. Nichols' (1960) light microscopic study of the tube-feet of



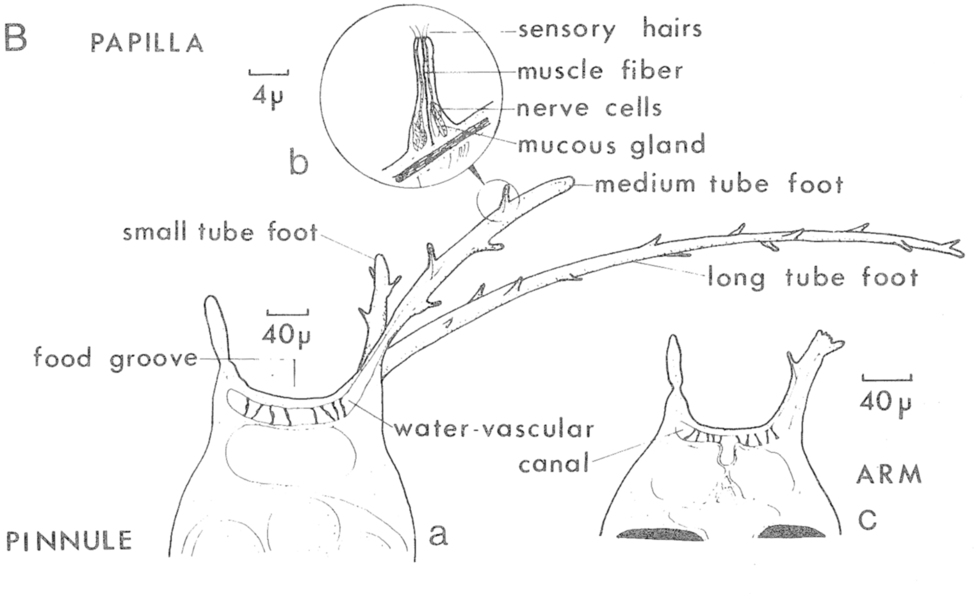


Figure 2A. Arrangement of the tube-feet along a crinoid pinnule; a) Plan view of a pinnule showing relationship between tube-feet (black) and lappets (stippled); b) Perspective view of part of a pinnule showing the angles at which tube-feet are held during feeding (lappets omitted); c) Transverse section across line CC in A, showing angles at which tube-feet are held in relation to lappets during feeding (after Nichols 1960).

Figure 2B. Morphology of the tube-feet and radial water vascular system in the comatulid crinoid *Antedon;* a) Transverse section of ambulacral part of a pinnule; b) Enlarged transverse section of a papilla; c) Transverse section of ambulacral part of an arm (after Nichols 1966a).

the comatulid *Antedon bifida* is the most comprehensive work available and is the basis for the following account. The tube-feet are arranged in groups of three (triads) along the ambulacral groove of each pinnule (fig.2a) and arm except near the mouth where they are single. These triads alternate along each side of the groove; each triad consists of a long, medium, and short tube-foot. Close observation of the tube-feet of 15 other comatulid species representing four families revealed a similar triad arrangement which is most likely common to all living crinoids (Meyer 1979). The long or primary tube-foot extends between the flap-like lappets, which are fused to the proximal parts of the medium and short tube-feet of each triad. Contraction of the medium and short tube-feet causes closure of the lappets over the ambulacral groove. In extended position, the primary tube-feet project laterally at a slight angle to the plane of the groove, while the medium tube-feet project at about 45 degrees to the groove and the short tube-feet stand roughly perpendicular to the groove (fig.2a).

The tube-feet are armed with papillae bearing terminal sensory hairs and containing mucus glands (fig.2b). Nichols (1960) reported a single muscle fiber within each papilla, but Holland's (1969) electron microscopic examination of the papillae revealed that the supposed muscle fiber in the comatulid *Nemaster rubiginosa* is a bundle of microtubules of uncertain function.

According to Nichols (1960), contact of food particles with the sensory papillae stimulates forcible ejection of mucus strands and lashing of the tube-feet inward toward the food groove. Food particles ensnared in mucus are passed from the long to the medium to the short tube-feet which pack the material into a mucus string within the groove. This string is transported along the groove of the pinnules and arms to the mouth by ciliary currents. I have frequently observed this string travelling along the ambulacral groove of crinoids feeding *in situ.* Thus, the characterization of crinoids as 'ciliary-mucus feeders' by Hyman (1955) seems justified, although it neglects the role of the tube-feet. Nichols (1960, 1966, 1972) used the terms 'food net' and 'mucus net' to describe the means by which food particles are trapped by the tube-feet. Subsequent authors have employed the term 'mucus-net feeding' to describe the crinoid feeding mechanism. This implies a weblike network of mucus strands extending over and between the extended tube-feet. While I have seen strands of mucus clinging to the arms and pinnules (see also Magnus 1963), there is no evidence of a weblike net. It is clear from Nichols' work that ejection of mucus strands is restricted to those tube-feet stimulated by particle contact, and that particles are not trapped by a preformed web of mucus. Other invertebrates such as tunicates, polychaetes, echiurids, and possibly pelecypods utilize a true mucus net or sheet in feeding (MacGinitie 1941, 1945, Monniot 1979), and thus application of the term 'mucus net' to crinoids should be abandoned because of its incorrect connotation for the feeding mechanism.

2.1.1. *Tube-feet as efficient filters*

Significant differences in spacing and length of the primary tube-feet in several sympatric comatulid species on Western Pacific reefs are correlated with feeding position and feeding posture (fig.3, Meyer 1979). Species having longer, more widely spaced tube-feet are generally those living semi-cryptically within the reef infrastructure, utilizing a multi-directional feeding posture. Crinoids with relatively shorter, more closely spaced tube-feet occur on elevated perches and utilize a filtration fan feeding posture (see section 2.2.). Similar studies by Liddell (1980) in the Carribean are in general agreement with these results.

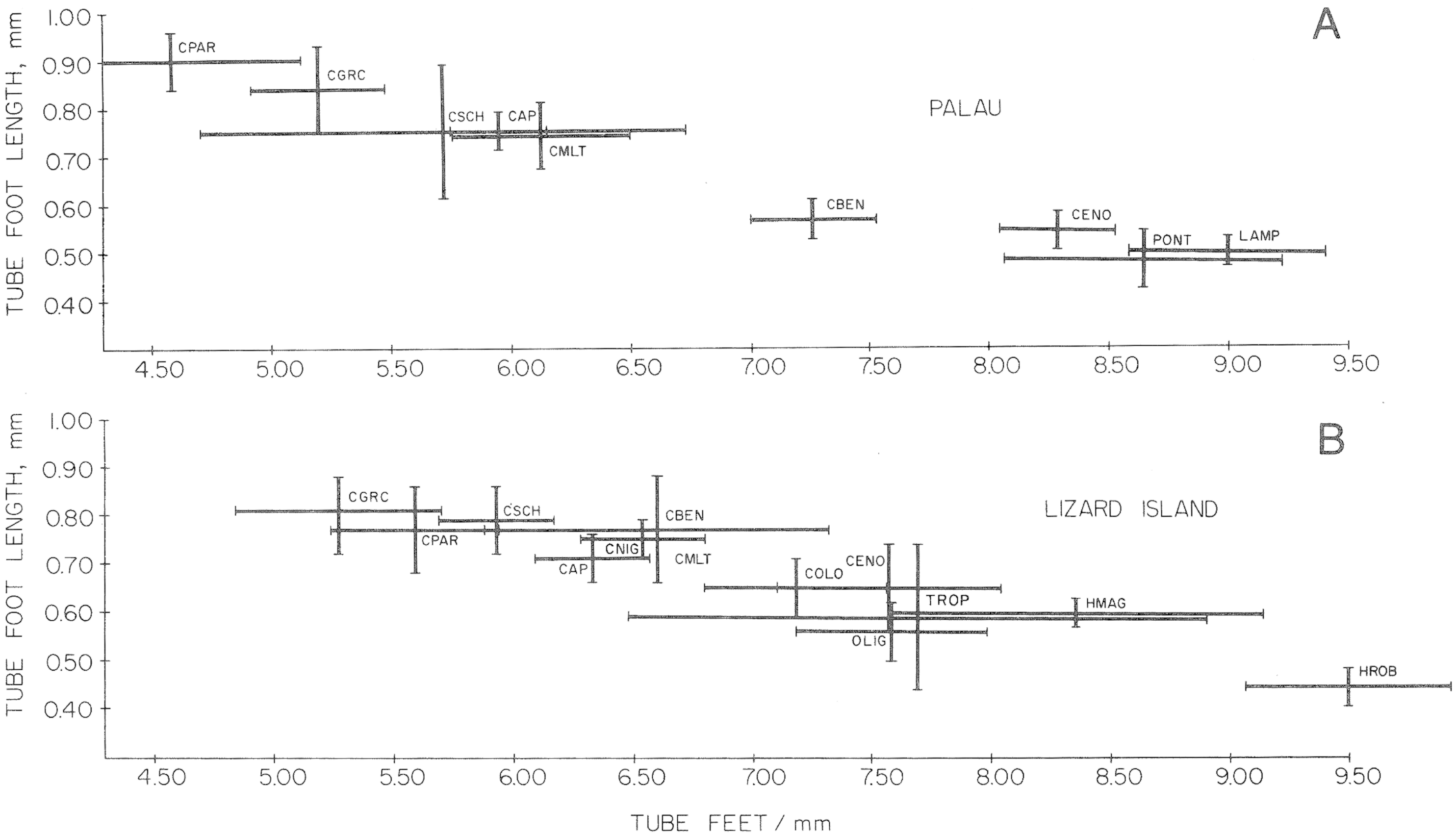


Figure 3. Relationship between spacing (abscissa) and length of tube-feet in comatulid crinoids. Plotted points are mean spacing and length with 95 % confidence intervals for each species. A. Crinoids from Palau Islands, Western Pacific; B. Crinoids from Lizard Island, Great Barrier Reef. Comasteridae: CPAR – *Comanthus parvicirrus*, CGRC – *Comaster gracilis*, CSCH – *Comanthina schlegeli*, CAP – *Capillaster multiradiatus*, CMLT – *Comaster multifidus*, CNIG – *Comatella nigra*, CBEN – *Comanthus bennetti.* Colobometridae: COLO – *Colobometra perspinosa*, CENO – *Cenometra bella.* PONT – *Pontiometra andersoni*, OLIG – *Oligometra serripinna.* Tropiometridae: TROP – *Tropiometra afra.* Mariametridae: LAMP – *Lamprometra palmata.* Himerometridae: HROB – *Himerometra robustipinna*, HMAG – *Himerometra magnipinna* (after Meyer 1979).

These observations on spacing and length of tube-feet combined with feeding habits can be interpreted in terms of aerosol filtration theory applied to biological filters by Rubenstein & Koehl (1977). Aerosol filtration theory holds that in lower velocity flows, particles are captured by mechanisms of gravitative settling and motile-particle deposition, but at higher velocities, particles are captured by mechanisms of direct interception and inertial impaction. In crinoid tube-foot filters, it seems reasonable to interpret increased length and spacing of tube-feet as adaptations to mechanisms of particle capture at lower velocity flows prevailing within the reef infrastructure. Decreased length and spacing of tube-feet, on the other hand, provide a denser filter which is more efficient for mechanisms of particle capture at higher flow velocities experienced by more exposed species (Meyer 1979). A further implication of aerosol filtration theory is that a filter of a particular morphology functioning against a given flow velocity will fractionate an optimal size range from the available population of particles. This has been experimentally demonstrated by LaBarbera (1978) for tube-foot suspension feeding by ophiuroids. If this prediction holds true for crinoid tube-foot filters, then interspecific differences in modal particle sizes can be expected for the diets of crinoids having differences in spacing and length of the tube-feet (Meyer 1979).

2.1.2. *Tube-feet in ancient crinoids*

There is but a single known case of possible preservation of tube-feet in fossil crinoids, and this is from the problematic, oldest known crinoid *Echmatocrinus* from the Middle Cambrian Burgess Shale (Sprinkle 1973). According to Sprinkle, these structures definitely represent original soft parts, but there is some question as to whether they are tube-feet or unplated pinnules. The presence of tube-feet in fossil crinoids is generally inferred for the following reasons: 1) An adoral groove is present along the arms and pinnules of fossil and Recent crinoids. As in Recent crinoids, it is thought that this groove carried extensions of the ambulacral tract and water vascular system in ancient forms (Ubaghs 1978). 2) In Recent forms imbricating series of soft lappets or ambulacral plates shield the tube-feet, with each lappet corresponding to a triad of tube-feet (Nichols 1960). Preserved ambulacral covering plates in fossil forms probably also shielded tube-feet, although this does not prove their existence. The adoral groove on pinnulars of the Recent stalked crinoid *Endoxocrinus* is scalloped by a series of lateral pockets which each correspond to a set of tube-feet (Macurda & Meyer 1975a, pl.24, fig.5). Similar structures in fossil crinoids would provide the best evidence for the presence of tube-feet, but as yet no such structures have been reported. It is likely that they have been overlooked.

2.2. *Feeding postures of pinnulate crinoids*

Observations of living crinoids *in situ* have demonstrated that crinoids are capable of modifying the posture of the arms and pinnules so as to take maximum advantage of the prevailing regime of water movement for efficient suspension feeding. The energetic advantages of adaptations that harness prevailing flow for feeding purposes have been discussed by Vogel (1978).

Initial observations of living crinoids in aquaria (Chadwick 1907, Gislén 1924, Nichols 1960) led to the idea that crinoids had a static feeding behaviour in which the oral side was directed upward and the arms formed a horizontal or conical collecting bowl. Crinoids were assumed to rely on a vertical rain of detritus as the principal food source. *In situ* observations made of deep-sea crinoids (Pérès & Picard 1955, Pérès 1958, 1959), shallow-water comatulid crinoids in the Red Sea (Magnus 1963, 1964, 1967, Fishelson 1968, 1974, Rutman & Fishelson 1969), comatulids in the Caribbean (Meyer 1972, 1973a, b, Macurda 1973, 1975, Meyer & Macurda 1976, Macurda & Meyer 1977, Liddell 1980), comatulids in the Western Pacific (Macurda & Meyer 1975b, 1976b, Meyer & Macurda 1977, 1980, Meyer 1979), temperate comatulids (LaTouche 1976, 1978), and deep-sea comatulids and stalked crinoids (Laborel *et al.* 1961, Marr 1963, Reyss & Soyer 1965, Macurda & Meyer 1974, 1976a) have revealed a complex range of crinoid feeding postures in response to rheophilic behaviour. The rheophobic collecting bowl is now relegated to some deep-sea crinoids and to certain ancient stalked forms (Breimer 1978).

2.2.1. *Behaviour in relation to flow velocity*

The feeding postures of crinoids vary in relation to both flow velocity and flow pattern (table 1). Several postures have been observed during conditions of slack current. In shallow-water comatulids the arms are usually held arched over the oral disk in a meridional fashion and the pinnules along each arm are non-planar (Meyer 1973a, fig.4-4, 5-2, Meyer & Macurda 1980, fig.4d). This was originally termed a radial posture (Meyer 1973a), although subsequent work has suggested that this description is better applied to a type of filtration fan (see below). LaTouche (1978) found that *Antedon bifida* forms what can be termed a cone posture during slack current. The arms are merely extended outward from the plane of the oral disk; and the pinnules are non-planar (LaTouche 1978, fig.3A, pl. IA, F, IIIC). This is similar to the collecting bowl described earlier, but it should be noted that this random arrangement of arms and pinnules is probably adapted to particle capture from low velocity multidirectional flow, not in response to a gravitative settling alone (LaTouche 1978:882). Adaptation to slight multidirectional flow also was suggested by Meyer (1973a: 113) for the meridional posture. Meyer noted that the tube-feet are extended in this posture, so that it should not be considered as an inactive resting position. The posture of deep-water comatulids during slack current has already been noted. In stalked isocrinids the oral side is directed upwards but the arms recurve aborally, giving the appearance of a wilted flower (Macurda & Meyer 1974, fig.1e). The comatulid *Pontiometra,* elevated on long, stilt-like cirri, assumes a similar posture (Meyer & Macurda 1980, fig.3c).

Crinoids respond to directional horizontal flow by aligning the arms into a filtration fan oriented perpendicular to the current. This behaviour was first observed by Pérès & Picard (1955) and has subsequently been observed in many other comatulids and stalked crinoids. The advantages of this planar orientation have been demonstrated experimentally by Leversee (1976) in gorgonians. The rate of particle capture is greatly enhanced by orientation normal to the flow direction. Crinoid filtration fans probably afford similar benefits. As a corollary to the general occurrence of filtration fans among crinoids, arms forming the fan

Table 1. Rheophilic crinoid feeding postures in relation to flow regime

Flow pattern	Relative flow velocity		
	~ 0	Low	High
Unidirectional or bidirectional	Horizontal, cone, meridional, droop	Filtration fans	Deflected fans windsock
Multidirectional		Multidirectional	

are nearly always oriented with the ambulacral groove facing downcurrent (Magnus 1963, Meyer 1973a, Macurda & Meyer 1974, LaTouche 1978). Some arms twist up to 180° to achieve this orientation. One advantage of this orientation may be that the open ambulacral groove is turned away from the direct impact of the current. A further advantage is related to the way in which the tube-feet transfer seized particles to the ambulacral groove, from the long, to the medium, to the short tube-feet. This region of transfer is placed in the 'lee' of the arm where a region of reduced velocity and microturbulence is created. This should facilitate the retention of particles seized by the long tube-feet and enhance capture by the shorter tube-feet by increasing the residence time of particles in the leeward microregion of the ambulacral groove. These interpretations have never been tested experimentally in crinoids, but similar effects have been suggested by Warner (1977) for gorgonians (termed 'leeward feeding') and demonstrated experimentally in gorgonians by Leversee (1976).

Orientation of the arms by crinoids is initiated by very slight flow velocities, although fan formation may not be complete until higher velocities are reached. The progressive response of crinoids to increasing flow rates has been described in different comatulids by Magnus (1963), Meyer (1973a), LaTouche (1978) and Meyer & Macurda (1980). The overall implication of these studies emphasized by LaTouche (1978) is that different orientations of the arms and pinnules are advantageous at different flow velocities. The optimal range of flow velocities in which a rheophilic crinoid functions is reflected in its skeletal morphology, with smaller, delicate forms best suited to regions of lower flow rates and larger, more robust forms better adapted to flow rates approaching 1-2 knots (50-100 cm/sec) (Meyer 1973a, LaTouche 1978).

Several types of filtration fans have been recognized among living crinoids (Meyer & Macurda 1980). Arcuate fans (fig.4a) are formed by comatulid crinoids that occupy a perch such as a coral or rock. Radial fans (fig.4b) are utilized by comatulids that cling to gorgonians or sponges in a position elevated above the sea floor in a manner of stalked crinoids. Some stalked crinoids may form a radial fan if the arms are extended laterally in the plane of the oral disk. Arm fans (fig.4e) are utilized by comatulids that attach with the cirri within crevices or beneath ledges, extending the arms from a restricted opening. Parabolic fans (fig.4c, d) occur in both comatulid and stalked crinoids when the arms curve aborally, forming a dish-shaped fan which is oriented with the concave side (abambulacral) upcurrent. Curvature of the pinnules into the current was also observed by Magnus (1963, fig.8b) in a comatulid which forms a planar filtration fan and by LaTouche (1978, pl.IB) in *Antedon*. My observations indicate that this is quite common among Pacific comatulids. In addition, the long tube-feet along each pinnule often curve back away from the ambulacral groove (LaTouche 1978, pl.IA, Meyer 1979, fig.1a). Warner (1977) has pointed out the occurrence of similar dish-shaped fan structures in other passive suspension feeders such as gorgonians that are oriented to unidirectional currents. Warner conducted experiments using models of parabolic vs. flat filtration fans which suggest that parabolic fans oriented concave toward the current capture more particles because they filter a greater volume of water. In the case of crinoids, it is apparent that a flat radial fan will have large gaps between the individual arm fans. Aboral curvature of the arms enables pinnules of adjacent arms nearly to touch, forming a continuous feeding net.

The formation of a common filtration fan by two or more conspecific individuals of comatulid crinoids has been reported by Magnus (1964, fig.7) and Meyer (1973a, fig.3-4). The increased density of overlapping arms and pinnules in these common fans may facilitate suspension feeding for the constituent individuals by creating a more pronounced baff-

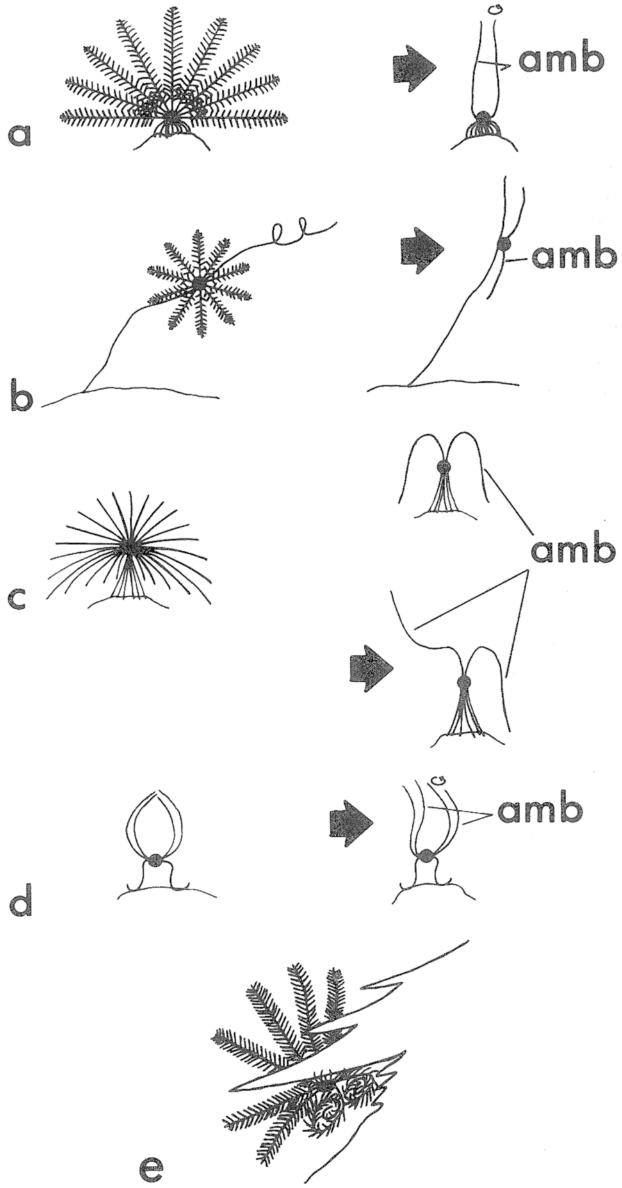


Figure 4. Diagrammatic sketches of the principal modes of filtration fan formation by comatulid crinoids; a) Arcuate fan. Left, view parallel to current direction; right, view perpendicular to current direction (large arrow); small arrow indicates twisting of downcurrent arms so that food grooves are downcurrent; b) Radial fan. Left, view parallel to current direction with crinoid attached to wire coral; right, view perpendicular to current direction (large arrow), with food grooves downcurrent; c) Parabolic fan. Right, top, view of crinoid with elongate cirri during slack current; below, view of same crinoid with current from left, showing uplift of arms on upcurrent side. Note that food grooves are downcurrent. Left, view downcurrent toward concavity of parabolic fan, with pinnules omitted; d) Arm postures of multibrachiate species that lack cirri. Left, view of meridional posture of arms during slack current, note elevation of calyx by arms; right, view of parabolic fan oriented to current from left; e) Arm fan. Calyx of crinoid is attached beneath ledge or within crevice; arms with planar pinnules are held normal to current or wave oscillation but fans of adjacent arms not always contiguous (a-d after Meyer & Macurda 1980).

ling of flow than does the fan of a single individual. The increased baffle-effect probably facilitates particle capture and retention within the dense fan (Meyer 1973a). In waters around the British Isles, the comatulid *Antedon bifida* forms dense aggregations although common filtration fans are not formed (Warner 1979). Warner suggested that the dense forest of arms in these aggregations may benefit feeding through a similar baffle-effect.

2.2.2. *Behaviour in relation to flow pattern*

Comatulid crinoids form bidirectional fans in response to oscillating water movement (Meyer 1973a, Meyer & Macurda 1976a, LaTouche 1978). In this posture, the ambulacra of some arms face one direction while others are 180° opposed; 180° arm twisting does not occur. The characteristic downcurrent orientation of the pinnular ambulacra is nevertheless maintained, because the pinnules with their extended tube-feet act like miniature weathervanes, swivelling passively near the base so that the ambulacra are always in the lee. Pinnules with different degrees of basal twist can be seen in *Antedon* as illustrated by LaTouche (1978, pl.IA). This is a further example of passive reorientation as discussed by Warner (1977).

Arm and pinnule postures adopted by fan-forming crinoids during slack current have already been discussed, but some crinoids prefer microhabitats that continuously experience multidirectional flow. These include particularly the semi-cryptic reef-dwelling comasterid comatulids (Meyer 1973a, b, Meyer & Macurda 1980) and antedonids like the cryptic *Ctenantedon* (Meyer 1972) and *Antedon* (LaTouche 1978) where it occurs in turbulent microhabitats. Semi-cryptic comasterids extend the arms at random without forming a fan and hold the pinnules fixed in two or more planes along each arm (multidirectional posture; see Meyer 1973a, fig.6-2). Pinnular swivelling also occurs. Antedonids are capable of modifying pinnule arrangement according to flow conditions (see LaTouche 1978, fig.2). These postures probably maximize exposure of the tube-foot arrays to varying flow patterns. Radial or three-dimensional growth forms among other passive suspension feeders have been interpreted similarly (Riedl 1964, Warner 1977).

In some situations, a single crinoid will utilize a combination of the filtration fan and the multidirectional posture. For instance, an arcuate fan may be formed by most of the arms, but those arms adjacent to the substratum hold the pinnules in a four-row arrangement in response to turbulence near the substratum (Meyer 1973a, fig.3-2). Likewise, in gentle currents arms on the downcurrent side of *Antedon* may hold the pinnules in a triplanar arrangement in response to turbulence created in the lee of the planar upcurrent arms (LaTouche 1978, fig.3C).

2.3. *Functional morphology of feeding appendages in fossil crinoids*

The information on the feeding behaviour of living crinoids has prompted many paleontologists to examine the feeding morphology of fossil forms. Breimer (1969) was the first to realize the implications of neontological information for fossil crinoids, and this was folowed by several contributions (Lane & Breimer 1974, Breimer & Webster 1975, Lane & Burke 1976, Meyer & Lane 1976) culminating with Breimer's comprehensive review (1978). Several reconstructions of feeding postures of ancient stalked crinoids have been attempted (figs.5,6) (Ettensohn 1975, Ausich 1977, Rasmussen 1977, Haugh 1979). Welch (1978) utilized scale models of the unusual Paleozoic camerate *Pterotocrinus* to simulate in a flume various possible feeding orientations. In all of these studies, the rheophilic nature of crinoids has been emphasized and the utilization of filtration fan feeding has been suggested.

While interpretation of the feeding habits of ancient crinoids has clearly benefitted from recent advances in knowledge of the living animal, paleontological studies have provided unique insight into synecological aspects of crinoid feeding. Lane (1963, 1973) documented the occurrence in the Mississippian (Lower Carboniferous) of North America of some of the most species-rich communities of crinoids known. A total of 19 species of stalked crinoids recorded from one community of the famous Crawfordsville (Indiana) fauna, represents an *in situ* burial of a living community (Lane 1973). The high species diversity and abundance of this assemblage prompted Lane to consider possible means by which so many species could coexist within this single 'guild' of epifaunal passive suspension feeders. Lane (1973) suggested the possible utilization of food particles of different sizes by different crinoid species. Meyer & Lane (1976) pointed out that Recent crinoids and basket stars (Ophiuroidea) utilize filtration fan feeding postures, but differ in the density of the feeding network as well as in mechanism of particle capture. Crinoids, having a finer-meshed feeding net, collect particles up to a few hundred microns in size, while basket stars with a coarser feeding net, collect particles over an order of magnitude larger than those taken by crinoids (Davis 1966, Macurda 1976). Similarities in the mode of arm branching between basketstars and certain Paleozoic crinoids led Meyer & Lane to suggest that these crinoids may have captured coarser particles than did crinoids with densely pinnulate feeding nets.

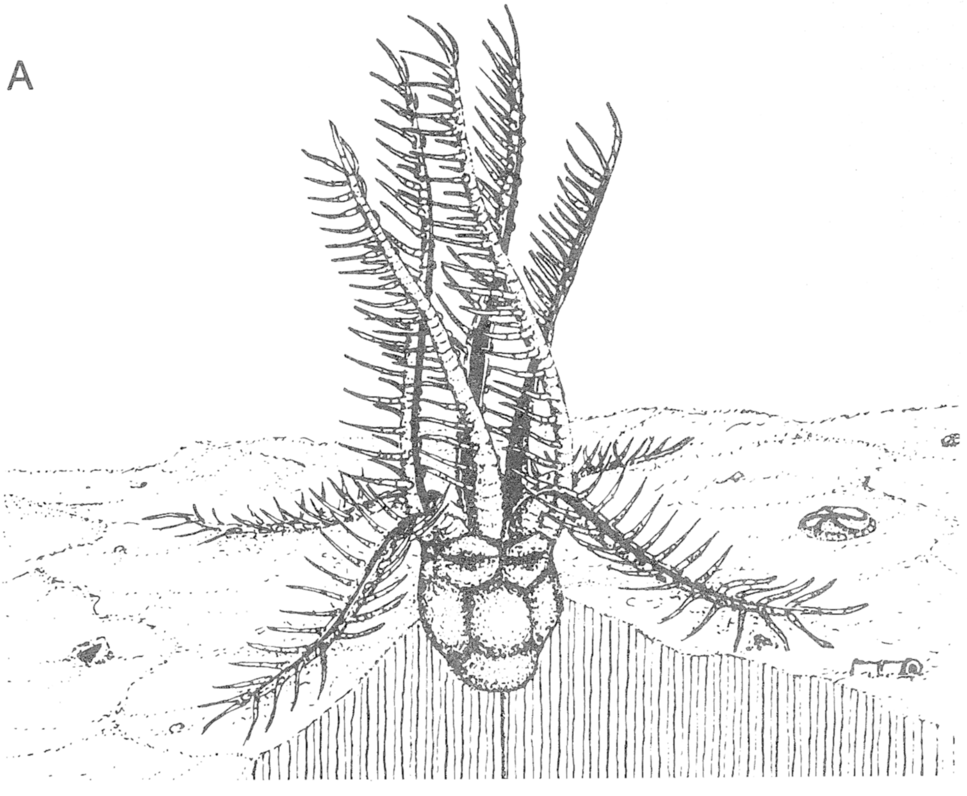
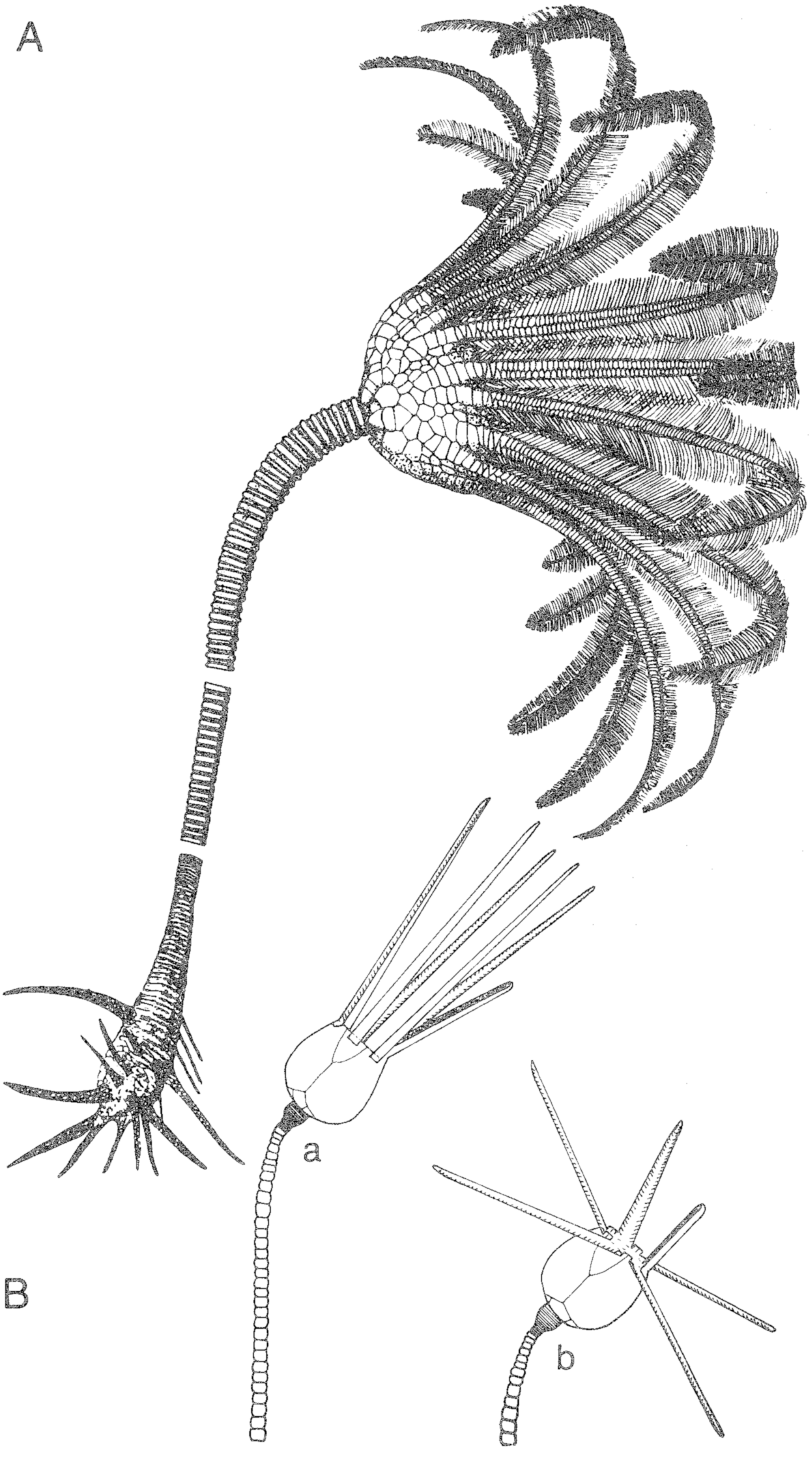


Figure 5a. Reconstruction of the mode of life of a Middle Paleozoic (Mississippian) stemless inadunate crinoid *Agassizocrinus lobatus.* Propped by shorter arms, calyx rests in a depression; longer arms form filtration fan against current inferred from lower right to upper left (after Ettenshon 1975).

The full implications of possible interspecific differentiation in size selection of food particles have been developed by Ausich (1980), who has examined the morphology of filtration fans within diverse Mississippian crinoid communities. Ausich measured stem length, width of the adoral groove, area of filtration fan, and number of branches in the fan of well preserved specimens representing a wide variety of crinoid taxa which occur sympatrically in these Mississippian communities. This analysis showed an inverse relationship between fan density (area divided by number of branches) and width of the adoral groove. Ausich expressed this relationship by plotting each taxon on a bivariate plot of fan density vs. width of the adoral groove and showed that the several taxonomic groups considered fall along an inverse hyperbolic curve referred to as a niche differentiation spectrum. While there is overlap between members of some groups, other groups are clearly isolated along this spectrum. Ausich interpreted this distribution in terms of theoretical predictions of the operation of biological filters developed by Rubenstein & Koehl (1977). The implications of this theory for filtration by the tube-feet of living crinoids have already been discussed. Applied to Ausich's niche differentiation spectrum, the theory predicts that crinoids with a particular fan density would have been optimally suited for capture of particles in a certain size range, and that this range would have differed from the optimal size range for other fan densities. Width of the adoral groove is closely related to width of the actual ambulacral groove which has been claimed to control the upper limit of particle size

Figure 5b. Reconstruction of the mode of life of Jurassic stalked crinoids (Isocrinidae, Pentacrinitidae). Parabolic filtration fans are based on observations of living stalked crinoids closely related to these Jurassic forms (after Rasmussen 1977). Alternatively, these same Jurassic crinoids have been interpreted to have been pendant from floating logs (see Seilacher *et al.* 1973, fig.1).


A
a
B
b

that can be accommodated by the crinoid feeding mechanism (Rutman & Fishelson 1969). Thus the inverse correlation between fan density and width of the adoral groove found by Ausich seems to substantiate the predictions of filtration theory and the concept that sympatric crinoid groups in these diverse Mississippian communities fed on different size ranges of particles. The similarity of Ausich's findings to those of Meyer (1979) based on studies of the tube-feet in living crinoids is striking and carries strong implications as to possible resource partitioning within diverse crinoid communities, ancient and modern.

2.4. *Feeding in non-crinoid crinozoans*

It is generally assumed that other extinct, non-crinoid crinozoans (paracrinoids, eocrinoids, blastoids, parablastoids, and 'cystoids') also lived as benthic passive suspension feeders, although many aspects of the functional anatomy of these groups are unknown. These echinoderms possessed arms or brachioles radiating from the theca which were presumably used in construction of a feeding net. For example, Breimer & Macurda (1972, figs.101, 102) reconstructed both rheophilic and rheophobic feeding habits for different blastoids on the basis of differences in the morphology of brachioles, theca, and column. Rheophilic habits were probably the most common mode of life in this group.

Sprinkle (1973) drew a fundamental functional morphological distinction between arms and brachioles. Arms, as found in crinoids and paracrinoids, are direct evaginations of the thecal wall (endothecal), often branched, which contain extensions of the coelomic, haemal, and water vascular canals. Brachioles, found in blastoids, parablastoids, rhombiferan cystoids, and eocrinoids, are exothecal structures arising from ambulacral areas recumbent on the theca; brachioles lacked extensions of the canal systems found in true arms but, like arms, they possessed an ambulacral groove with covering plates. Sprinkle maintained that tube-feet did not line the ambulacra of brachioles, although the ambulacra may have been ciliated. The distinctions between arms and brachioles formed the principal grounds for Sprinkle's (1973) recognition of a subphylum Blastozoa, composed of the blastoids, parablastoids, rhombiferan cystoids, and eocrinoids.

On the other hand, Breimer & Macurda (1972) interpreted the morphology of blastoids to include tube-feet originating from water canals coursing over the ambulacral areas of the theca, although not extending onto the brachioles. The primary food gathering mechanism of blastoids may have been muco-ciliary (Sprinkle 1973), and the role of the tube-feet, if present, was possibly secondary. Tube-feet in living echinoderms have an auxiliary respiratory function, but Nichols (1972), noting the presence of elaborate structures such as blastoid hydrospires and 'cystoid' pore systems supposedly devoted to respiration, suggested that tube-feet in these ancient echinoderms may have been much less well developed. If this were so, it would be necessary to identify a food gathering mechanism that did not rely on tube-feet in these extinct groups. While it is tempting to assume that the tube-foot mechanism found in living crinoids was present in ancient crinoids and other crinozoans, the possibility of other mechanisms cannot be overlooked.

Figure 6a. Reconstruction of the mode of life of a Lower Paleozoic (Ordovician) camerate crinoid, *Rheocrinus aduncus,* showing parabolic filtration fan; current inferred from left (after Haugh 1979).
Figure 6b. Reconstruction of feeding postures for the Paleozoic (Silurian) inadunate crinoid *Pisocrinus;* a) Conical filtration fan; b) Planar filtration; note erect anal tube (after Ausich 1977).

3. FOOD COMPOSITION

The morphology and rheophilic behaviour of crinoid tube-feet, ambulacra, arms and pinnules clearly indicate that crinoids are adapted to the capture and utilization of minute particulate material (Fell 1966a). There do not seem to be any reasons for doubting that crinoids have been microphagous throughout their evolutionary history. It is more difficult to specify the types of particles actually ingested and utilized by crinoids. Available information comes entirely from analyses of the composition of gut contents and fecal material. Limitations of this sort of information should be realized (Steele-Petrovich 1976). First, because the tube-feet probably capture both organic and inorganic particles indiscriminately, gut contents will include indigestible as well as digestible particles. Second, differential digestion of particles will remove many food items from gut contents even before defecation. Third, much material in the gut or feces may escape notice or be unidentifiable, representing undigested remnants of food items or indigestible detrital material. Thus studies of gut contents and fecal material can provide only a partial indication of the diet of crinoids. Potential utilization of the various types of particulate material can only be evaluated by experimental studies of digestion and assimilation, and these have been virtually lacking.

A.H.Clark (1921) and Gislén (1924) reviewed earlier reports on the gut contents of crinoids and presented qualitative data for several genera. Analysis of diatoms, found in gut contents, performed for Gislén by Cleve-Euler, revealed a high proportion of benthic species. Gislén concluded that 'crinoids live upon a mixed diet of detritus and benthonic microorganisms and plankton, but that the detritus-nourishment plays a very important part, at least for some of them' (1924:279). Gislén believed composition of the food varies with the type of bottom, as did Carpenter (1884), but also depends on the available plankton. Fell (1966a, table 2-1) summarized available records of crinoid gut contents and suggested that 'the limiting factors in determining food organisms would seem to be mainly size (determined by the diameter of the food groove) and availability in the selected habitat'.

Rutman & Fishelson (1969) made monthly quantitative analyses of the gut contents of the Red Sea comatulid *Lamprometra klunzingeri* over a year. The average diet is made up of about ten per cent phytoplankton, 50 per cent protozoans, and about 40 per cent crustaceans and mollusks. The diatoms and tintinnids were dominated by typical benthic forms, supporting the findings of previous workers on the importance of resuspended benthic material in the gut contents. No data were presented on the abundance of detritus. Seasonal changes were thought to reflect fluctuations in the available plankton, although no data were given on composition of ambient plankton.

A similar year-round quantitative study was made by LaTouche (1976) for the temperate comatulid *Antedon bifida* in Irish waters. LaTouche reported (1976:199): 'The food was found to consist largely of resuspended material from the sea floor approximately 65 per cent (yearly average) of this being organic detritus (principally of faecal origin), 17 per cent silt and fragmented diatom frustules, and 18 per cent diatoms or dinoflagellates'. Experiments showed that *A.bifida* was unable to digest most of the diatoms and dinoflagellates found in the gut, but that microbial populations within the organic detritus may provide the major food source. This is the only investigation which has addressed the problem of determining the actual nutritional value of materials found in the gut contents, and its results call into question all previous statements made as to the nature of the 'diet' of crinoids and the contribution of various planktonic groups found in the gut contents. However, because siliceous frustules and chitinous carapaces, as well as calcareous tests and shells are probably indigestible by crinoids, their proportions in gut and fecal samples probably reflect the proportions ingested and analysis of these items can assess their potential contribution to the diet.

3.1. *Interspecific comparison of crinoid gut contents*

Although suspension feeders are generally regarded to be non-selective, there is increasing evidence that there is size fractionation of available particles which is dictated by differences in filtration morphology and feeding behaviour (Rutman & Fishelson 1969, Meyer & Lane 1976, LaBarbera 1978). Differential size fractionation may occur between major groups of suspension feeding echinoderms, for example crinoids and basket stars (Meyer & Lane 1976), but fractionation within a group has not been demonstrated. Rutman & Fishelson (1969) stated that three co-occurring Red Sea comatulids seemed to feed on the same food items. Examination of gut contents and fecal material from sympatric species of Western Pacific comatulids indicates that variation in taxonomic composition of identifiable food items among samples from a single crinoid species may equal variation among species (personal observation). On the other hand, food particle size distributions indicate possibly significant differences between crinoid species which may be a consequence of interspecific differences in spacing and length of the tube feet observed by Meyer (1979).

3.2. *Dissolved nutrient uptake*

The direct absorption from sea water of dissolved nutrients such as amino acids and carbohydrates has been recognized as a potential source of nutrient for echinoderms as well as other marine invertebrates (Binyon 1972a, West *et al.* 1977, Bamford, chapter 13). Uptake of amino acids and glucose by the arms and cirri of the comatulid *Leptometra phalangium* was demonstrated by West (1978), who suggested that the cirri obtain significant nutrition from higher dissolved nutrient concentrations near the substratum. Lane & Breimer (1974) suggested that uptake of dissolved nutrients may be the principal mode of feeding in larval crinoids which have not developed arms, but this has not yet been verified. None of these studies has assessed the concentrations of dissolved nutrients in the habitats of crinoids, and thus the actual significance of this phenomenon remains to be demonstrated.

4. CONCLUSIONS

Among the echinoderms, crinoids are the most conservative in terms of feeding mechanisms. Unlike other echinoderm classes which have diversified each into more than one major mode of feeding, crinoids have probably existed as passive (hence rheophilic) suspension feeders throughout their 500 million year evolutionary history. The tube-foot feeding mechanism has been used to extract the smaller size fractions of the plankton and suspended matter. Particle selectivity is limited by the width of the ambulacral groove and the ability of the tube-feet to retain active plankters (Rutman & Fishelson 1969). Spacing and length of the tube-feet may also control particle size (Meyer 1979). There is no evidence of particle selection within the size range utilized. Crinoids probably overlap with many other benthic invertebrates in terms of particle sizes and types captured.

Although the method by which crinoids trap and ingest particles has apparently been uniform within the group, there has been considerable diversification in adaptation to feeding within different microhabitats. The principal axes of crinoid feeding niches appear to be type of substratum, elevation above substratum, feeding periodicity, and water movement regime. Morphological, physiological, and behavioural adaptations have enabled crinoids to exploit a wide range of microhabitats defined by these (and undoubtedly other) ecologic axes.

What are some of the major unanswered questions concerning the feeding biology of crinoids? Although a good deal is known of the feeding mechanism and feeding habits of crinoids, virtually nothing is known of their nutritional requirements. There is little published information on their digestive processes (Anderson 1966, Binyon 1972a, Lawrence & Lane chapter 15). Of the various components of crinoid gut contents, which are actually assimilated and contribute to the energy budget? What is the role of dissolved nutrient uptake in crinoid nutrition?

Questions on an ecological scale focus on the diverse and abundant communities of crinoids that now exist on coral reefs and existed in other environments in the geologic past. Has this diversification been a consequence of competitive pressures from crinoids and other organisms, or is it unrelated to competition? Do the adaptations of sympatric species of crinoids to different feeding habits and microhabitats contribute to resource partitioning within these complex communities? What is the role of crinoids in the trophic web of reefs and level bottom communities where they are abundant? Do dense aggregations of crinoids create unique conditions that provide a mutually beneficial feeding environment for their constituents? Finally, what ecological factors accounted for the great diversity and abundance of ancient crinoids, and for their decline?

ACKNOWLEDGEMENTS

I thank W.I.Ausich, R.W.LaTouche, D.B.Macurda jr, B.West and the editors for criticism of the chapter; J.Carrol for typing the manuscript; the National Science Foundation (NSF Grant DEB 76-24334) for financial support in preparation of the chapter.

CLAUDE MASSIN

3

FOOD AND FEEDING MECHANISMS: HOLOTHUROIDEA

Holothuroids collect food only by means of their buccal tentacles. They can be deposit-feeders or suspension-feeders as defined by Walker & Bambach (1972). These different feeding mechanisms involve different tentacle forms (fig.1). Some nutrients are obtained also by epidermal absorption of dissolved organic matter (see Bamford, chapter 14).

1. DEPOSIT-FEEDING HOLOTHUROIDS

The disposit-feeders collect sediment and particles with their buccal tentacles on soft or hard bottoms. On soft bottoms the tentacles dig into the sediment as is the case for the funnel-feeders and the conveyorbelt-feeders, or take only the surface layer, raking the sediment (rake-feeders). On hard bottoms (rocks or algae) the tentacles sweep and pick up particles from the surface (surface-feeders). The latter are similar to the ooze-feeders described by Yamanouchi (1939). Several types of tentacular behavior can occur in the same species.

The sediment ingested by deposit-feeding holothuroids is composed mainly of: a) inorganic compounds (silica and/or limestone), b) organic detritus, i.e. dead and decaying animal or vegetal matter, c) micro-organisms (bacteria, diatoms, protozoans, cyanophyceans, foraminiferans) associated with inorganic compounds and detritus, and d) fecal pellets of other animals (Hauksson 1979, Khripounoff 1979, Traer 1980) or their own fecal pellets (Bakus 1973, Powell 1977, Sloan & Von Bodungen 1980). Ludwig (1889-92), Oomen (1926b) and Bakus (1968, 1973), among others, give a detailed list of intestinal contents.

Deposit-feeding holothuroids feed mainly on sediment-associated micro-organisms, particularly on bacteria (Bakus 1968, 1973, Yingst 1976, Moriarty 1978). These holothuroids also swallow foraminiferans (Bakus 1968, Barth *et al.* 1968), some cyanophyceans (Sournia 1976), diatoms (Lanzi 1904) and meiofauna (Renaud-Mornant *et al.* 1971, Renaud-Morant & Helléouet 1977, Khripounoff 1979).The latter generally are rare in intestinal contents (Renaud-Mornant & Helléouet 1977, Hauksson 1979). Bacterial populations will influence the distribution of holothuroids in a benthic area. The relationships between deposit-feeders, bacteria and sediment are extraordinarily complex and will not be discussed here (for information see Newell 1965, Fenchel 1967, 1969, 1971, Bianchi & Massé 1974, Dale 1974, Gray 1974, Rhoads 1974, Billen 1976).

The gut of deposit-feeding holothuroids sometimes is full of large fragments of sea grass (Oomen 1926b, Massin & Jangoux 1976). These plants are not digested (as Yingst 1974, demonstrated with *Parastichopus parvimensis*) but support epiphytic organisms on which the holothuroids feed.

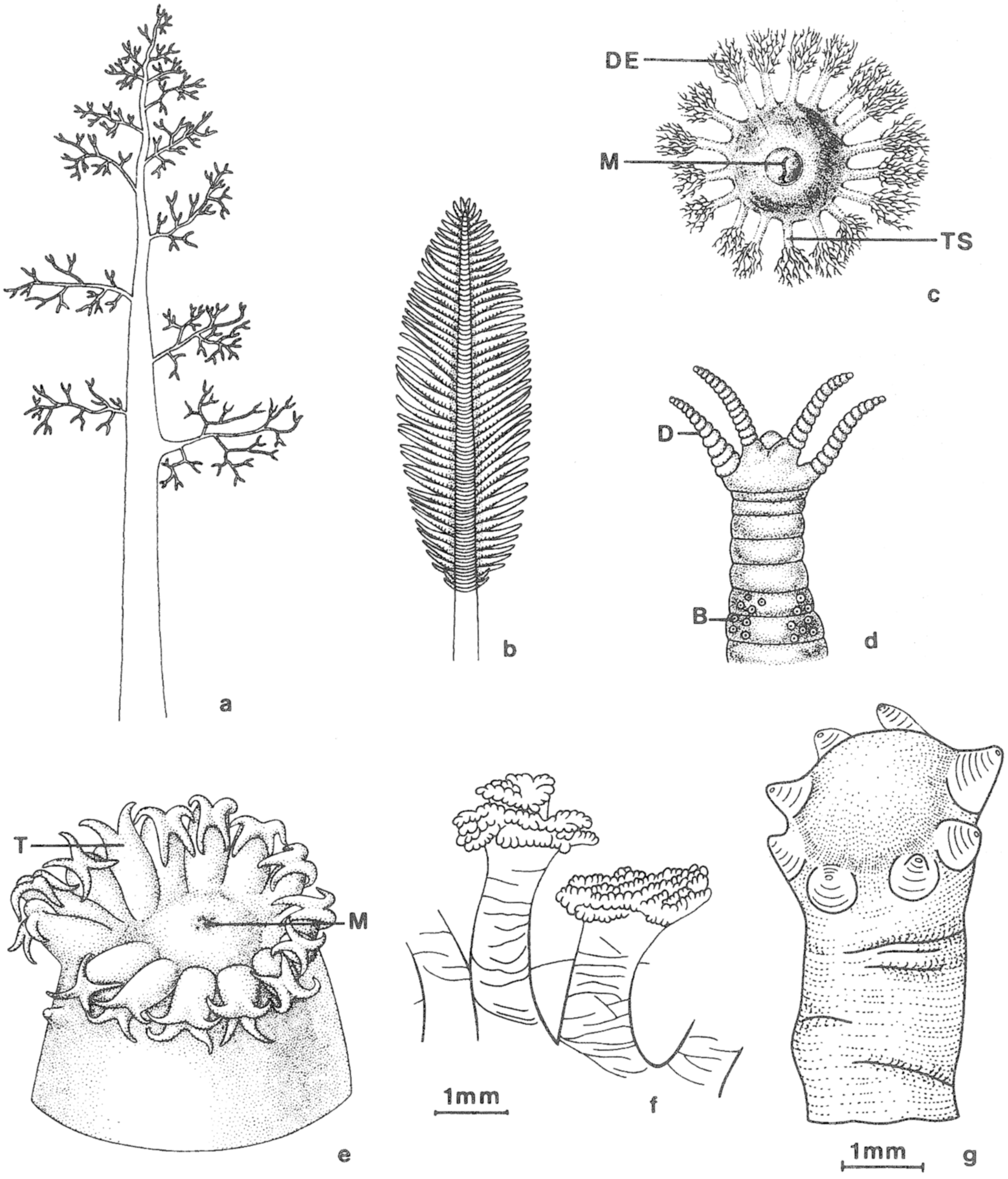


Figure 1. Tentacle types: a) Dendritic (mainly dendrochirotes); b) Pinnate (synaptids); c) Pelto-dendritic: shaft of peltate tentacle but dendritic-like end in place of a disc. DE – dendritic end; M – mouth; TS – tentacle shaft (aspidochirotes: *Dendrothuria similis,* after Koehler & Vaney 1905); d) Digitate. B – buds or pits; D – apical digitations (synaptids: *Labidoplax digitata,* after Hamann 1884); e) Digitate. M – mouth; T – tentacle (molpadids: *Caudina arenata,* after Gerould 1896a); f) Peltate (aspidochirotes and some elasipods: *Ophnurgus glaber,* drawing from a photo in Hansen 1975); g) Digitate (elasipods: *Oneiroplanta mutabilis).*

1.1. *Dendrochirotida*

Two closely related Phyllophoridae have been described as plant-eaters on the basis of observations of the intestinal contents: *Pattalus mollis* (Semper 1880, in Ludwig 1889-92) and *Athyonidium chilensis* (Pawson 1964). In the case of *A.chilensis,* animal debris also was found in the digestive tract. These two species would be described more correctly as deposit-feeders than plant-eaters. They presumably feed on epiphytic micro-organisms. No information is available on the movements of the dendritic tentacles when collecting large debris (up to 42 x 6 mm and 25 x 10 mm, according to Pawson 1964).

1.2. *Dactylochirotida*

Dactylochirotes possess digitate or pennate tentacles. Their biology is poorly known. This is especially true for the Rhopalodinae, a family of bottle-like holothuroids with the anus close to the mouth. Dactylochirotes are believed to live mainly burrowed in the sediment. There is no information on their feeding habits. They are listed here only because they live in mud and their tentacles are not well suited for suspension-feeding.

1.3. *Aspidochirotida*

The majority of aspidochirote holothuroids live on the sediment surface. They swallow the upper few millimeters of sediment with their peltate tentacles (fig.1f) and make no or very light trails. Only some deep-sea aspidochirotes make deep furrows in the sediment (*Pseudostichopus villosus,* Lemche *et al.* 1976). *Holothuria scabra, Bohadschia vitiensis* and *Bohadschia bivittata* can burrow in the sediment, but not to collect food. They are basically rake-feeders (Yamanouchi 1956).

Aspidochirotes feed continuously (Yamanouchi 1939, 1942, Trefz 1958, Bonham & Held 1963, Massin 1978, Mosher 1980) or have a daily rhythm in their feeding frequently related to light levels (Crozier 1918, Yamanouchi 1939, 1956, Crump 1965). In addition to a daily rhythm, some aspidochirotes (mainly stichopodids) possess a seasonal rhythm and stop feeding during the summer (e.g. *Stichopus japonicus,* Mitsukuri 1903, Tanaka 1958a, Choe 1963). This period of starvation can be accompanied by evisceration (e.g. *Stichopus regalis,* Bertolini 1930b, 1932; *Parastichopus californicus,* Swan 1961b; *Stichopus tremulus,* Jespersen & Lutzen 1971).

Aspidochirote rake-feeders creep on the bottom with the mouth down (Trefz 1958). The tentacles, fully extended with spread tips, sweep the bottom and act as shovels when the sediment is swallowed. Each tentacle, without a defined order, pushes sand into the mouth in which the sphincter opens and closes regularly. According to Delage & Hérouard (1903) and Cherbonnier (1954) sand grains and alimentary particles adhere to the tentacle as a result of mucus secretions. On the other hand, Trefz (1958, *Holothuria atra*) and Massin (1978, *Holothuria tubulosa*) observed that grains are not held together with mucus and stick only weakly to the tentacles. According to Roberts (1979) holothuroids pick up particles by mechanical ensnarement. There are internodular spaces on the sensory zones or nodules of tentacular tips which trap the particles when the tentacle retracts.

When feeding, selection of grain sizes by holothuroids generally is low (Bertram 1936, Yamanouchi 1939, Yingst 1974). Only Hauksson (1979), working with *Parastichopus tremulus,* found a positive selection of coarser particles. Contrary to the assertion by Trefz (1958) and Bakus (1973), holothuroids would be able to choose the organically richest

Table 1. Relative concentrations of organic matter in the surrounding sediment and in the sediment contained in the pharyngeal bulb

Species	Material measured	Surrounding sediment	Pharyngeal content	References
Holothuria atra	Carbon	1	34	Webb *et al.* 1977
Id.	Nitrogen	1	3	Webb *et al.* 1977
Id.	Bacterial biomass	1	3 to 5	Moriarty 1978
Holothuria tubulosa	Total nitrogen	1	6	Cohnheim 1901
Id.	Total organic matter	1	2 to 3	Massin 1980b
Id.	Protein	1	2 to 5	Massin 1980b
Stichopus japonicus	Total nitrogen	1	3 to 5	Tanaka 1958a

sediment (chemical selection). There is very often a clear increase of organic matter concentration between the bottom sediment and the material found in the pharyngeal bulb (Hauksson 1979, and table 1).

Some holothuroids apparently do not concentrate organic matter in the upper part of the gut. Yingst (1974) found only a ten per cent increase in *Parastichopus parvimensis.* She ascribed it to pharyngeal mucus secretions. The phenomenon of concentration of organic matter in the upper part of the gut which frequently implies that the feces are richer than the surrounding medium, is very frequent in deposit-feeding organisms (Hylleberg 1975, Hylleberg & Galluci 1975). The concentration of sediment rich in organic matter in the upper part of the gut implies that the buccal tentacles must recognize and select special particles. Therefore buccal tentacles must possess chemosensitive zones. These zones may be located at the apical tentacular buds or nodules as described by Jourdan (1883), Hamann (1884) and Roberts (1979).

Some aspidochirotes are conveyor belt-feeders (e.g. *Holothuria arenicola,* Gardiner 1904, MacNae & Kalk 1962, Mosher 1980; *Holothuria pervicax,* MacNae & Kalk 1962). *H.arenicola* lives preferentially in muddy areas where strong currents occur and where the sea grass *Thalassia testudinum* grows; it lies obliquely in the sediment at a rather shallow angle to the surface and ingests sediment below the surface but no deeper than 15 to 20 cm (Mosher 1980). No detailed information is available on their tentacular movements when feeding.

1.4. *Elasipodida*

Many elasipods feed like aspidochirotes. They possess peltate tentacles either very similar to those of aspidochirotes (fig.1f), or with an end-disc bearing more or less developed finger-like processes (fig.1g) (Hansen 1975). According to many deep-sea photographs, Elasipoda are primarily rake-feeders (Barham *et al.* 1967, Heezen & Hollister 1971, Pequegnat *et al.* 1972, Menzies *et al.* 1973, Lemche *et al.* 1976), grazing the uppermost sediment surface and leaving no or light traces (Kitchell *et al.* 1978).

Elasipods are also able to concentrate in their pharyngeal bulb the sediment fractions richest in organic matter. The latter is five to eight times more concentrated in the upper part of the gut than in the surrounding sediment (Sokolova 1958, Bordovsky *et al.* 1974, Khripounoff 1979). As for shallow-water holothuroids the capacity to concentrate is more or less developed. According to Sokolova (1958), the more complicated the macroscopic structures of the tentacular apex, the greater the selectivity by the holothuroid. Nothing is known of the tentacular movements and selection process. Aside from the chemical selection, some elasipods (e.g. *Psychropotes longicauda, Benthogone rosea* and *Paroriza pallens*) exert a slight physical selection of the sediment, swallowing the finest grains (Khripounoff 1979).

Some elasipods are occasionally scavengers: *Scotoplanes* sp. is attracted by the remains of fish (Pawson 1976), some species are attracted by baits (Hessler 1972), *Peniagone* sp. has been captured in a baited trap (Laubier & Sibuet 1977), and Khripounoff (1979) has found large pieces of macrofauna (holothuroids, polychetes, ophiuroids) in the intestinal contents of abyssal holothuroids (e.g. *Benthogone rosea*).

Food is scarce in the abyssal ecosystem, and Rowe (1974) supposed that holothuroids must ingest large amounts of sediment to meet their metabolic needs. However, food is not always a limiting factor. The amount of food available, e.g. in the Cape abyssal plain (South Atlantic ocean) and the Biscay abyssal plain (North Atlantic ocean), is the same but the biomass is 16 orders of magnitude higher in the latter; the limiting factor being probably the proportion of carbonates in the sediment (Khripounoff, unpublished).

1.5. *Apodida*

The apodids are surface-feeders, rake-feeders or funnel-feeders. When funnel-feeders, they act as a conveyor belt-feeder (Powell 1977). The surface-feeders (e.g. *Synaptula hydriformis, Opheodesoma spectabilis* and *Opheodesoma grisea*) feed mainly on diatoms, algae, small crustaceans and worms, detritus and all that can be removed from the substratum (H.L.Clark 1896, 1898, 1907, Olmsted 1917, Berril 1966, Roberts 1979). Generally they do not ingest sediment. Abyssal forms (e.g. *Myriotrochus* sp., Heezen & Hollister 1971) could also be rake-feeders, but generally live buried in the substratum (Hansen 1975).

The external surface of the tentacles of *Trochodota dunedinensis* and of *Opheodesoma spectabilis* secretes mucus and is sticky (Pawson 1963, Berril 1966). According to Berril (1966) the tentacles are applied to the substratum or are coiled around sea grass. Once loaded with food, the movements of the tentacle are: extension (a few seconds), a decrease in size and retraction of the tentacle to the mouth (fig.2), insertion of pinnules into the mouth, withdrawal of the tentacle cleaned by the buccal sphincter, extension of the tentacle. This sequence of movements takes approximately 15-20 seconds (Berril 1966). Gotto & Gotto (1972) also measured a time of 20 seconds for the tentacular movement of *Labidoplax media.* There is no special order in tentacle contractions, but generally the two tentacles on either side of a contracted tentacle are extended.

The funnel-feeding synaptid (*Leptosynapta tenuis,* Powell 1977) and minute synaptids

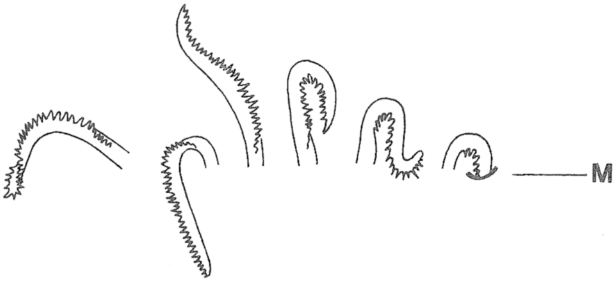


Figure 2. Tentacle movement of *Opheodesoma spectabilis.* M – mouth (after Berril 1966).

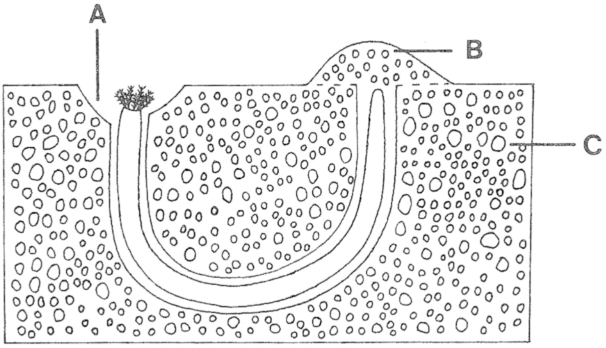


Figure 3. *Leptosynapta tenuis* in a typical feeding position in its U-shaped burrow (after Powell 1977) A – funnel shaped depression; B – fecal mound; C – sediment.

(*Psammothuria ganapatii,* Rao 1968; juvenile *Patinapta ooplax,* Rao 1973; *Rhabdomolgus ruber,* Menker 1970) frequently live in coarse sediment where the silt/clay proportion is low (0,3-7 %). The sediment preference of these synaptids could be linked to the fact that this sediment is well-sorted (apodous holothuroids, e.g. *Chirodota rigida,* dig more efficiently in such sediment, Lawrence & Murdoch 1977). For the minute synaptids, which belong to the mesopsammal fauna, coarse sediment is preferred because the spaces between the sand grains are more important. The mesopsammal synaptids ingest almost exclusively the particles around the sand grains and not the sand grains themselves (Menker 1970). Thus we can consider them as surface-feeders. The funnel-feeders swallow sediment and feed on the associated organic matter and micro-organisms. As for the surface-feeders and the rake-feeders, the external part of the tentacles is sticky and collects particles (Pourtales 1851, H.L.Clark 1899b). According to Powell (1977), four different feeding modes exist for *Leptosynapta tenuis* (in every case, the particles that stick to the tentacles are ingested): 1) The synaptid when in a U-shaped burrow (fig.3) sticks out its oral end and plows its tentacles along the surface of the sediment forming star-shaped surface feeding traces. Sand is ingested as the trace is made. 2) A funnel-shaped feeding hole is formed. Sediment slides down from the surface and is ingested at the bottom of the funnel. 3) Sediment is ingested while burrowing. 4) The synaptid moves to the bottom of a vertical shaft and then moves upward again ingesting grains from the side of the burrow wall.

Leptosynapta tenuis feeds mainly on the top 5 mm of sediment, i.e. the richest in organic matter. The sediment ingested below this first half centimeter must be ascribed mainly to burrowing activity and not to feeding activity. Granulometry of surrounding and intestinal sediment is slightly different in *L. tenuis.* This is not the result of a choice but the interaction of the relative accessibility of grains and the feeding mechanism used (Powell 1977).

1.6. *Molpadida*

The biology of molpadids is poorly known because most of them live at a depth of more than 100 m and are buried in the sediment. They are conveyor belt-feeders, lying either vertically (i.e. *Molpadia oolitica*) or obliquely (e.g. *Paracaudina chilensis* and *Molpadia roretzii*) in the sediment (Rhoads & Young 1971, Yamanouchi 1926, 1929, Hatanaka 1939). The feces are not voided as castings but as a cloud of sand, building a fecal mound around the holothuroid tail (fig.4). Very little information is available on tentacular move-

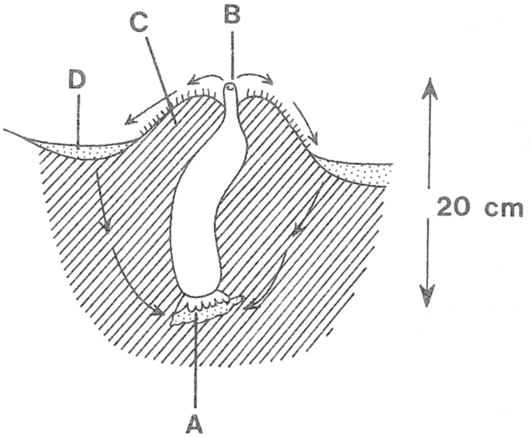


Figure 4. Diagrammatic representation of feeding position of *Molpadia oolitica.* (after Rhoads & Young 1971). A – Mouth; B – anus; C – fecal mound; D – unconsolidated feces.

ments. According to MacGinitie & MacGinitie (1968), *Caudina arenicola* pushes its tentacles (fig.1e) ahead into the mud and particles of detritus are entrapped by mucus and swallowed. Sediment selection is low, either chemically (Sokolova 1958) or physically (Khripounoff 1979). Molpadids live in finer sand than apodids (*Molpadia oolitica* lives in sediment where silt/clay proportion is higher than 65 %, Rhoads & Young 1971).

2. SUSPENSION-FEEDING HOLOTHUROIDS

The food of suspension-feeding holothuroids is composed of small plants (diatoms, unicellular algae) and animals (protozoans, nematodes, copepods, ostracods, jelly-fish and larvae), and suspended organic matter associated or not with inorganic material (Ludwig 1889-92, Pearse 1908, Eichelbaum 1910, Blegvad 1914, Hunt 1925, Hyman 1955, Brumbaugh 1965, Reese 1966, MacGinitie & MacGinitie 1968, Hunter-Rowe *et al.* 1976, Fankboner 1978). This agrees with the general food sources cited by Jørgensen (1966) for suspension-feeding organisms. Among the food cited, diatoms are the most important. According to Jørgensen (1966), the latter are a very important source of food for suspension-feeders because they do not possess such a thick cell wall as other algae. Suspended organic matter represents only 10-20 % of holothuroid food requirements (Brumbaugh 1965). Some suspension-feeders are necrophagous: Arnaud (1973) captured *Psolus charcoti, Heterocucumis denticulata, H.vaneyi* in baited traps, and *Heterocucumis coatsi* with fishing-line.

Holothuroids, contrary to many other suspension-feeders, do not produce a water stream when feeding but exhibit a rheophilic behaviour. In relation to this, there is also an acrophilic behaviour which increases exposure to the currents (Fedra 1977). The stickiness of holothuroid tentacles is low and mobile organisms can escape. Consequently, holothuroids catch prey which are immobile or only slightly mobile.

2.1. *Dendrochirotida*

2.1.1. *General position of the tentacles*

Dendrochirote holothuroids live on hard substrates (on rocks, in crevices, under boulders) or on soft substrates (buried in the sediment or lying on the surface). On both substrates, they passively extend their tentacles into the water (Ludwig 1889-92, Blegvad 1914, Könnecker & Keegan 1973) and/or brush the bottom with them (Grave 1905, Blegvad 1914, Smith 1962). In relation to their rheophilic behaviour some (e.g. *Ocnus planci*) are able to orient their tentacles when feeding, the tentacular crown facing the current (Olscher & Fedra 1977). On hard substrates, two more elaborate postures can be adopted. The tentacular crown forms an open-mesh cup in *Psolus chitinoides* (Fankboner 1978). Once food is within range, the tentacles may seek out food by vigorous movements. This implies chemosensitivity. Alternatively, expanded tentacles are bent inwards so that they overlap to form a semi-closed cup-shaped meshwork (Fankboner 1978). This position promotes ensnarement of relatively large inanimate material.

2.1.2. *Tentacular movements*

Tentacular movements of the dendrochirotes have been described by many authors (for papers before 1885 see Ludwig 1889-92, Hérouard 1890, Petersen 1893 in Eichelbaum 1910, Grave 1905, Pearse 1908, Van der Heyde 1923a, Klugh 1923, Hunt 1925, Smith 1962, Brumbaugh 1965, Fish 1967b, Schaller 1973, Könnecker & Keegan 1973, Jordan 1973, Sutterlin & Waddy 1976, Hunter-Rowe *et al.* 1976, Olscher & Fedra 1977, Fankboner 1978). These holothuroids possess ten dendritic tentacles (fig.1a) which are not always of equal length. Generally *Thyone* spp. and some *Cucumaria* spp. possess two shorter forked ventral tentacles (8 + 2 tentacles).

When feeding, holothuroid tentacles are fully expanded. Individual tentacles regularly shrink, are brought back near the mouth, bend and are inserted into the mouth. The buccal sphincter closes around the base of the tentacle. The tentacle is held a short time in the mouth before being withdrawn and fully expanded again. This behaviour occurs with *Cucu-*

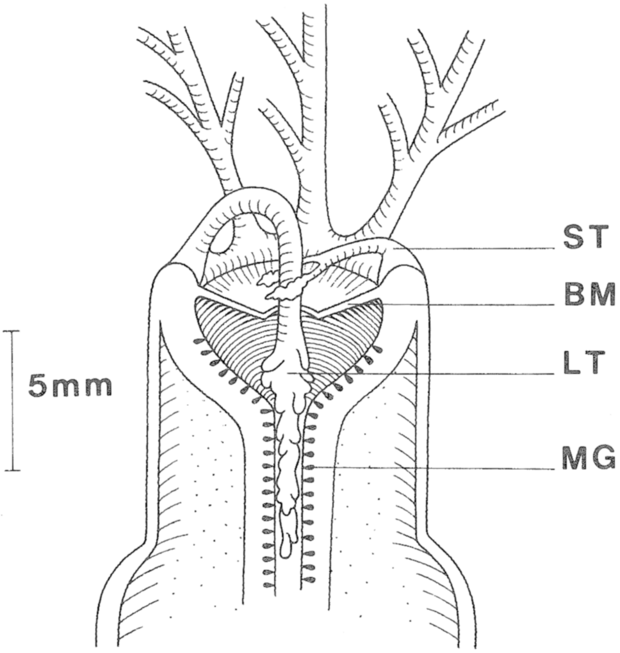


Figure 5. Tentacle movement of *Trachythyone elongata* (schematic cut of anterior body part). BM – buccal membrane; LT – long tentacle; MG – mucus glands; ST – short tentacle (after Fish 1967b).

maria frondosa and *Psolus chitinoides* (Sutterlin & Waddy 1976, Fankboner 1978).

When a holothuroid possesses two small ventral tentacles, these can act either in co-operation with the large tentacles (e.g. *Thyone fusus,* Hunter-Rowe *et al.* 1976; *Sclerodactyla briareus,* Van der Heyde 1923a; *Trachythyone elongata,* Fish 1967b), or independently (e.g. *Aslia lefevrei* and *Pawsonia saxicola,* Schaller 1973). In the case of co-operation, a small tentacle is held over the mouth so that its forked end surrounds and wipes the large tentacle as it is withdrawn (fig.5). The small tentacle is then inserted into the mouth.

Neopentadactyla mixta, which possesses 20 tentacles, has 15 large ones peripherally arranged around the mouth and 5 smaller ones which form an inner circlet (Könnecker & Keegan 1973). The large tentacles collect food as those of species of *Cucumaria* or *Thyone.* One (sometimes two or three) of the five smaller tentacles follows a larger one into the pharyngeal cavity and is thought to remove food material from the large tentacles (Könnecker & Keegan 1973).

Schaller (1973), Sutterlin & Waddy (1976) and Hunter-Rowe *et al.* (1976) numbered the tentacles and noted the sequence of penetration in the mouth. These authors pointed out that a tentacle is almost never inserted twice in succession into the mouth. When tentacles are of equal length, as in *Cucumaria frondosa,* they are inserted one after the other into the mouth but adjacent ones are not inserted in sequence. In the case of holothuroids with two small forked tentacles, as *Aslia lefevrei, Pawsonia saxicola* and *Thyone fusus,* adjacent tentacles very often are inserted consecutively into the mouth.

The analysis of the sequence of tentacle insertion in the mouth indicates that some sequences occur more frequently than others. Very often two opposite tentacles follow one another, but this phenomenon undergoes many individual variations. Statistically, all tentacles are used with equal frequency. Sutterlin & Waddy (1976) were unable to formulate a mathematical expression of these observations. It was possible only to predict what tentacles might be moved in the next sequence.

Tentacle movement can occur uninterrupted (Ludwig 1889-92) but this does not imply a continuous feeding. *In situ* observations in the Mediterranean Sea on *Ocnus planci* indicate that tentacles are active for more than 95 % of the total time (Olscher & Fedra 1977). Their movement can be interrupted when the density of suspended food is several orders of magnitude greater than normal. Usually inactive periods (with the tentacles retracted) are caused only by the proximity of motile animals (e.g. fish, crabs). Tentacular activity of *O.planci* depends on food supply.

A feeding periodicity has been recorded for some species. Hunter-Rowe *et al.* (1976) observed that *in situ* feeding of *T.fusus* occurs in periods of 2-3 hours. They pointed out that the feeding rhythm is related to the strength of current flow and not with tide or light levels. As in stichopodids, in addition to a daily rhythm, some dendrochirotes possess a seasonal rhythm and stop feeding during the winter time (e.g. *Trachythyone elongata,* Fish 1967b).

2.1.3. *Food catching*

Food catching by dendrochirote tentacles has been considered for a long time as a passive phenomenon involving mucus secretions. However, Fish (1967b) noted the absence of mucus glands on the tentacles of *Trachythyone elongata.* He concluded that tentacular mucus comes from pharyngeal mucus glands. According to Fish, the tentacle is loaded with mucus when it is inserted into the digestive tract (if correct, a part of the mucus would be lost in the digestive tract because the tentacle is wiped by the buccal sphincter when it is withdrawn). Brumbaugh (1965) observed the lack of mucus glands on the tentacles of some dendrochirotes but noted the presence of terminal sticky papillae on which food could be fixed. These papillae provide the only sticky surface on the tentacle. Fankboner (1978) also noted the lack of mucus and mucus glands on the buccal tentacles of *Psolus chitinoides.* Only some special tentacular zones or buds are able to collect food. These buds are located on the apex of the tentacle branches and bear papillae which secrete mucus. These buds can also entrap food by mechanical action. When the tentacle is fully expanded, clefts or crevices of the bud are open; when the tentacle is contracted, particulate material passing through the tentacular crevices is caught. Tentacles bearing entrapped food release this material in the mouth. The material captured by the papillae also is released in the mouth with the help of the papillary ciliated cells. The buds act as a chemoreceptor as, according to Schaller (1973), the movement of the tentacles into the mouth occurs only if trapped particles have nutritional value. This indicates that holothuroid tentacles are able to make a choice, testing the chemical value of a particle. On the other hand, it must be noted that tentacle withdrawal is a reflex action which can happen even if the tentacle touches neutral particles (e.g. sand).

2.2. *Aspidochirotida*

Aspidochirotes possess peltate tentacles with some exceptions, e.g. *Holothuria glaberrima* which has dendritic-like tentacles (fig.1f) which are extended for suspension feeding (Nutting 1919, Lewis 1960, Lawrence & Kafri 1979). Other species are suspension-feeders (e.g. *Holothuria cinerascens*) and feed during the incoming tide (Sloan 1979). However food catching must be different from a dendrochirote. Indeed Sloan (1979) found that the size of inorganic particles in the gut of *Afrocucumis africana* (dendrochirote) differs appreciably from those of *H.cinerascens* (aspidochirote), although these two species are coexisting suspension-feeders. Hansen & Madsen (1956) suggested that *Galatheothuria aspera,* which is partially pelagic, feeds on suspended matter on the basis of its intestinal contents and the presence of dendritic-like tentacles.

2.3. *Elasipodida*

Pelagothuridae include pelagic species, some of which reach the abyss (Lemche *et al.* 1976). *Pelagothuria natatrix* and *Enypniastes ecalcarea* possess tentacles with forked dendritic tips (Heding 1950, Hérouard 1923, Gilchrist 1920). Others (e.g. *Enypniastes globosa* and *Enypniastes eximia*) possess tentacles which end in a fringed disc (Mitsukuri 1912, Hansen & Madsen 1956). Observations on the intestinal contents suggest that they are partly plankton-eaters (Kemna 1906, Gilchrist 1920), but there is no information on food collecting mechanisms.

Some Elasipoda with peltate tentacles can be suspension-feeders (e.g. juveniles of *Benthodites typica, Peniagone diaphana* and *Psychropotes longicauda* which are pelagic, Hansen 1975). *Peniagone diaphana* is also pelagic as an adult and feeds on suspended particulate matter (Barnes *et al.* 1976).

2.4. *Apodida*

Many burrowing and free living synaptids exhibit rhythmic tentacular movements. Tentacles are inserted into the mouth one after the other (e.g. *Leptosynapta inhaerens,* Cherbonnier 1953). In comparison with dendrochirotes, Becher (1907) and Olmsted (1917) suggested that this behaviour corresponds to suspension-feeding. However, Cherbonnier (1953) did not believe that these rhythmic tentacular movements are feeding movements.

3. DISCUSSION AND CONCLUSION

3.1. *Food*

Shallow-water holothuroids do not have different feeding behaviour potentials as do asteroids or ophiuroids. When there is no interspecific competition, one species occupies a variety of habitats and is able to exploit a range of different food sources (Sloan & Von Bodungen 1980). When several species co-occur, each occupies a well-defined ecological niche and, even if trophic category is similar, captured food is different and competition between species minimal. This fits Kohn's (1978) suggestion that particle feeders partition the habitat rather than food resources. In contrast, abyssal holothuroids are more opportunistic feeders (Sibuet 1980). This variability in feeding behaviour would result from the low amount of food available on deep-sea bottom.

Bacteria seem to be the main food of deposit-feeding holothuroids. In fact they are probably the most important intermediary between organic matter and compounds assimilated by the holothuroid. These bacteria are very often more abundant in intestinal sediment than in the surrounding sediment. In addition, it has been found that intestinal bacteria from deep-sea deposit-feeders (including holothuroids) have a different activity than bottom bacteria (Bensoussan *et al.* 1979, Bianchi *et al.* 1979, Josse 1979). However, it has not yet been demonstrated that these bacteria are specific to the digestive tract. Studies of gut bacteria and of the organic compounds they use would allow a more exact knowledge of what holothuroids assimilate from ingested food. Strangely enough, this aspect of holothuroid nutrition has been considered almost exclusively for abyssal species and remains to be evaluated for shallow-water forms.

In sandy or muddy biotopes, the nutritional composition of the sediment (richness in bacteria and organic matter) will be one of the important factors in determining the distribution of adult holothuroids. In rocky biotopes where there is little sediment, numerous microhabitats seem to be more important than the amount of food available.

Diatoms are the main food of suspension-feeding holothuroids. This means that they depend on phytoplankton for food. As plankton production frequently diminishes or ceases during some period of the year, suspension-feeders must reduce their metabolic need, stop feeding or seek other food sources (Jørgensen 1966). What is the response? Some suspension-feeding species stop feeding during winter time (see section 2.1.2.), but the majority feed all year. As they are able to brush the bottom with their tentacles, there may be an alternation or a combination between suspension- and deposit-feeding. The combination of the two feeding mechanisms could promote stability and density of holothuroid populations as is the case for *Lanice conchilega* (polychaete, Buhr & Winter 1977). Thus it would be interesting to know if the proportion of bottom material (bacteria, organo-mineral aggregates) and suspended organic matter in the intestinal content of holothuroids increases with decreases in plankton abundance.

Food types could also vary in the intestinal contents because the suspension-feeders collect particles at different levels in the water column according to whether they live in the sediment or fixed on rocks. Quality and quantity of collected particles would also vary with intensity and direction (unidirectional, oscillating, turbulent conditions) of water flow. We have little, if any, information on the relation between the intensity of current, the layer of water column exploited and the intestinal content of suspension-feeding holothuroids.

The occasional necrophagy of some holothuroids (mainly elasipods) suggests that they possess chemosensitive organs which are presently unknown.

3.2. *Feeding mechanisms*

There are no organs other than buccal tentacles involved in the feeding mechanism. The tentacular movements are very similar in the different orders of holothuroids: the tentacle first fully extends, the apical part shrinks, the tentacle bends and is inserted into the mouth. When withdrawn, the tentacle is wiped by the buccal sphincter and sometimes by other tentacles.

The mechanical shovelling described by Hyman (1955), Trefz (1958) and Bakus (1973) does not explain the physical or chemical selection of particles by deposit-feeding holothuroids. Among detritus-feeding holothuroids there is generally an important increase in organic matter concentration between the material in the pharyngeal bulb and the sediment. The higher concentration of organic matter in the pharyngeal bulb implies that holothuroids are capable of a chemical selection. Therefore holothuroids probably can be considered as selective feeders (chemically, but not mechanically), contrary to the opinion of Bakus (1973) and Walker & Bambach (1974). This selectivity implies the existence of chemosensitive zones on the tentacles; the study of their fine structure must be done.

The general opinion that food particles stick to the tentacle only by means of a mucus coating is not well supported. As pointed out by Fankboner (1978), it '. . . could be misleading because it may be taken to imply that all holothuroids possess sticky tentacles and that the stickiness is a property of the whole tentacle surface and not confined to a specific site'. Food capture of fine particles for both suspension-feeders and deposit-feeders may be the result of two processes: a) Food particles stick to specialized zones of the tentacle, the buds. b) Food is caught by mechanical ensnarement in bud crevices and tentacular apex crevices when the tentacle shrinks. This means that differences in food capture could be ascribed partly to the fine structure of the collecting zone. Large particles would not be involved in these phenomena as they are supposed to be ingested with the aid of several tentacles.

The class of holothuroids show a high degree of adaptative radiation in feeding mechanisms. This adaptive radiation is also developed within an holothuroid order (table 2). Molpadids seems to be the most specialized (perhaps also the dactylochirotes, but there are no data). Aspidochirotes present the highest adaptative radiation with the corresponding greatest variability in tentacle forms. Dendrochirotes, which include the most primitive holothuroids (Frizzel *et al.* 1966), live in very different biotopes, but their feeding mechanism and their tentacle forms do not undergo variations.

The elasipods, living on the uniform soft abyssal bottom, present a high variety of tentacle type. Sokolova (1958) found a correlation between the shape of the tentacular end-disc and the degree of selectivity in feeding, but Hansen (1975) found no relation between tentacle type and type of intestinal contents. We need more data on abyssal benthic life to know if there really is a correlation between intestinal contents and tentacle type and if the latter corresponds to an adaptation to microhabitats.