

To Dr. K. Baba  
with thanks for your help.  
Yours sincerely,  
Torben Wolff

## MACROFAUNAL UTILIZATION OF PLANT REMAINS IN THE DEEP SEA

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### SARSIA



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Plant remains of terrestrial, shallow-water, or epipelagic origin (wood, leaves, fruits, seagrass, and *Sargassum*) are abundant in many areas of the deep sea. Collections of plant material from the Caribbean area (>1200 m) have been examined. Fragments of wood and blades and rhizomes of seagrass (*Thalassia testudinum*) are particularly abundant in the Puerto Rico and Cayman Trenches into which they are transported by turbidity flows. The study has revealed a rich fauna which is listed together with previous, scattered records of association between deep-sea animals and plant remains.

About 50, mainly sessile, organisms utilize seagrass and wood as a substrate. Most common are byssus-producing mytilid bivalves. Polychaeta is the dominating group seeking shelter under bark and in cavities in wood (more than 25 species), and 10 species of isopods were found in hollow rhizomes (about 50 specimens of one species).

Several animal groups utilize plant remains as food. The opportunistic boring bivalves (*Xylophaga*) are for the first time recorded attacking seagrass rhizomes. Cocculinid gastropods (at least 9 species) are so abundant that it may be justified to regard them as another example of opportunistic species in the deep sea. Chitons and limpets are probably also herbivorous, and so are several species of polychaetes (mainly Nereidae), a remarkable echiuran worm, several species of amphipods and isopods, more than 10 echinoids (although mainly from the upper bathyal zone) and perhaps a few ophiuroids and asteroids.

It is suggested that the main nutriments for the herbivores, as in shallow-water areas, are provided by bacteria and fungi and possibly by their grazers. The discrepancy of data on growth rate and substrate conversion of bacteria in the deep sea may be attributable to several factors, e.g., the availability of energy, the stimulating effect of macrofaunal consumers, and the apparent age or residence time of deep water masses. The extremely rapid settlement of *Xylophaga* larvae indicates an even faster deterioration by bacteria or fungi or both.

The macrofaunal herbivores represent the final link in the decomposition food chain. They are available as prey for predators and as dead remains for scavengers, and their fecal pellets can be utilized by deposit feeders.

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### INTRODUCTION

Several of the great oceanographic expeditions have reported on the occurrence of remains of terrestrial plants in the deep sea. The *Challenger* found plant debris at 9 stations at 1500-3900 m depth, mainly near the Philippines and New Guinea, and a rich fauna at most of these localities (MURRAY 1895). Similar observations were made by the *Blake* in the West Indies, the *Albatross* in the East Pacific, and the *Siboga* in Indonesian waters (AGASSIZ 1888, 1892; WEBER 1902). A log of pine wood, several metres long, was collected by the *Ingolf* at 1800 m in the North Atlantic (K.W. Ockelmann pers. commn). During the Galathea Expedition records were

made of all remnants of plants from deep water. They occurred at no less than 56 stations (BRUN 1959), i.e. more than half of the successful trawlings carried out. At 4 stations in Indonesian waters the volume exceeded 1000 cm<sup>3</sup>, and in the Gulf of Panama a huge log was brought up. Most abundant were branches and twigs, followed by wood pieces, bark, and fruits (op. cit.).

Seagrass and *Sargassum* were not recognized as significant components of plant remains in certain deep-sea areas until deep-water photography became a scientific tool. Seagrass blades appeared on photographs from the Puerto Rico Trench, the Gulf of Mexico, and the Southwest Pacific (PRATT 1962; MOORE 1963; PEQUEGNAT

& al. 1972; LEMCHE & al. 1976). Based on a photographic survey, MENZIES & ROWE (1969) mapped the quantitative distribution of turtle grass (*Thalassia*) from the shelf to the abyssal plain off North Carolina. In nearly every one of about 5300 bottom photographs in the Virgin Islands Basin (average depth 3900 m), ROPER & BRUNDAGE (1972) observed seagrass remnants, particularly manatee grass (*Cymodocea*).

Clumps of *Sargassum* have been photographed at abyssal depths (SCHOENER & ROWE 1970; ROPER & BRUNDAGE 1972); numerous tracks around such clumps may suggest that they serve as a source of food (op. cit.).

Based on the wood and fruit remnants collected by the *Galathea*, KNUDSEN (1961) described no less than 17 new species of the boring bivalve genus *Xylophaga* from depths between 915 and 7290 m, thus more than doubling the number of known species. Apart from this study, no detailed examination of larger quantities of plant remains of terrestrial and shallow-water origin has hitherto been carried out.

## MATERIAL AND METHODS

During participation in 1973 as a guest in Cruise 14 of R/V *Akademik Kurchatov* in the Caribbean and adjacent seas I investigated the large amounts of plant remains collected in deep-sea trawlings, mainly in the Puerto Rico and Cayman Trenches (Table 1). The remains consist primarily of turtle grass, *Thalassia testudinum* (Pl. 1A), with a total wet weight of c. 1560 g and an average wet weight per station of c. 120 g (Table 1). Other seagrasses (e.g. *Cymodocea*) and *Sargassum* are insignificant. Plant material of terrestrial origin comprises lumps and pieces of wood (from 60 × 12 cm in size to tiny fragments), twigs, pieces of bark, leaves, husks of coconuts, other fruits, *Spartina*, *Phragmites*, and unidentifiable pieces of straw.

Inquiries for possible additional material in East American marine laboratories resulted in the loan of a large collection of plant remains from the School of Marine and Atmospheric Science, Miami. It was collected by R/V *Pillsbury* between 1964 and 1971 at 32 stations in the Caribbean area<sup>1</sup> at depths exceeding 1200 m (Table 1). The total volume (in alcohol, not compressed) is 5.1 litres of seagrass rhizomes and blades (almost exclusively *Thalassia*), 2.7 l of wood fragments, twigs, and bark, 0.6 l of fruits, leaves, and straw, and 0.05 l of *Sargassum*. The total wet weight of *Thalassia* is 631 g, of wood, twigs, etc. 1015 g (Table 1).

<sup>1</sup> By mistake, the shipment also contained plant material from St. 526 in the Gulf of Panama and St. 53 in the Gulf of Guinea. The location was not recognized until after polychaetes, molluscs, etc., from these stations had been identified. They have therefore been included here.

Table 1.

Station No.	Locality		Depth (m)	Wet weight (g)	
	N	W		<i>Thalassia</i>	Others
Off Georgia					
P120	31°48'	76°32'	2288	50	1
North of Bahama Islands					
P187	27°26'	77°50'	1373	5.5	2
North of Cuba					
P634	23°32'	82°39'	1661	4.5	0
P1444	22°24'	75°26'	2450	48	3
P1138	20°53'	74°20'	2747	13	11
P1435	21°58'	73°42'	1650	0	10.5
Puerto Rico Trench					
AK1181	19°56'	68°20'	5220-5300	<1.0	.
AK1189	19°39'	68°18'	7950-8100	30	.
AK1183	19°38'	67°46'	8330	140	.
AK1187	19°24'	68°00'	5890-6000	50	.
PL168	19°43'	67°05'	7965	311	10
PL384	19°45'	67°00'	7938	39	0
P811	19°26'	66°24'	7471	60	0.5
P993	19°24'	66°11'	7430	45	87
Northern Caribbean					
P631	18°27'	85°54'	4374	.	.
AK1272	20°08'	84°30'	4580	275	.
P577	19°48'	83°30'	4417	29	0
PL238	18°16'	78°31'	1537	9.5	9.5
PL235	17°54'	78°25'	1428	0.5	0.5
PL178	19°14'	73°14'	1760	0	595
Cayman Trench					
AK1243	19°01'	80°35'	6840-6850	150	.
AK1258	19°14'	80°30'	4600-4650	70	.
AK1259	19°06'	80°30'	5800-6500	200	.
AK1242A	19°01'	80°30'	6800	275	.
AK1269	19°24'	76°38'	5250-5280	30	.
AK1266	19°45'	76°43'	5900-6300	.	.
AK1267	19°39'	76°37'	6740-6780	200	.
Southern Caribbean					
P328	09°55'	79°02'	2071	.	.
P338	09°58'	78°31'	1827	0	25.5
P782	12°02'	73°26'	2365	1	2.5
P770	12°59'	71°44'	1308	1	2.5
P719	11°39'	64°35'	1517	0	137
Near Lesser Antilles					
PL401	17°51'	65°04'	4180	7	0.5
P976	17°35'	61°21'	3852	6	0
P892	14°18'	60°45'	1235	0.5	5.5
P905	13°46'	61°05'	1326	0.5	6
AK1207	13°27'	62°19'	2970-3000	0	.
P844	11°37'	60°12'	1656	0	19
Off Guiana					
P682	07°35'	56°21'	1326	0	52
P672	07°37'	55°24'	1278	0	1
P675	08°33'	54°18'	1253	0	11
Gulf of Panama					
P526	06°51'	79°28'	3197	0	.
Bay of Guinea					
P53	04°50'	04°58'	1549	0	25

← Table 1. Location and depth of *Akademik Kurchatov* (AK) and *Pillsbury* (P) stations providing plant material utilized by deep-sea animals. Approx. wet weight of *Thalassia* at AK stations and wet weight of *Thalassia* and remaining plant material at P stations.

Each fragment was examined under the microscope for epifauna, and rhizomes, straw, twigs, and pieces of wood were carefully split. Some *Thalassia* rhizomes were so fresh that they were solid throughout; they contained only one kind of animal, viz., boring bivalves. All other animals occurred in rhizomes whose interior was more or less decomposed, being entirely hollow or with a marrowlike material. Old *Xylophaga* cavities in wood and spaces between the bark and the wood were occupied by several kinds of animals.

In addition, reference has been made to various deep-sea animals from the Galathea Expedition and other sources which were associated with wood and have not previously been recorded in the literature.

## RESULTS

Preliminary results of the examination of seagrass collected by the *Akademik Kurchatov* were presented at a seagrass symposium in 1974 (WOLFF 1976). A more general treatment of seagrass utilization, including the *Pillsbury* material, was later prepared (WOLFF 1979). References to details and illustrations in these two papers are found in Table 2 and are summarized below.

### *Animals using plant material as a substrate*

**Protozoa: Foraminiferida.** Attached to the inner wall of *Thalassia* rhizomes at three stations are apparently live specimens of *Cibicides* sp. (some contain a greenish plasma), three black Allogromiida, and two agglutinating organisms referable to foraminiferans.

On wood from St. P1444 is one specimen of the deep-sea genus *Gyroidina* and from Sts P187, P719, P1178, P1435, and P1444 large numbers of apparently live *Tiphrotrocha* sp. (Pl. 1B). This genus is primarily known from shallow-water vegetation, but the abundance of the present species seems to indicate that it occurs in deep water.

**Xenophyophoria.** The first known instance of a xenophyophore using a solid substrate (a *Thalassia* rhizome) is *Semipsammina fixa* (TENDAL 1975).

**Coelenterata: Actiniaria.** Fixed to seven *Thalassia* rhizomes and one blade are 50 *Bathydactylus* (probably *B. valdiviae*).

**Turbellaria: Neorhabdocoela.** Species of Fecampidae are internal parasites in crustaceans. The female of *Kronborgia spiralis* attaches its spiral cocoon filled with egg capsules to the exterior of its isopod host (CHRISTENSEN 1976, fig. 7). A rather similar cocoon was found attached to a rhizome from 3852 m depth (Pl. 1C). Another cocoon on bark (St. P1178, 1760 m) is bottle-shaped, 1.9 mm long, and filled with about 200 capsules (Pl. 1D); it is referable to *Fecampia* (A.M. Christensen pers. commn).

Although Fecampidae have so far been known only down to 700–800 m, it seems obvious that the two cocoons were produced by deep-sea turbellarians (WOLFF 1979).

**Acoela.** Since this group has never been recorded beyond the shelf, it is doubtful whether an empty, acoele cocoon from 4417 m depth, although found attached to the inside of a hollow rhizome, is actually of deep-sea origin.

**Annelida: Polychaeta.** Live specimens and empty tubes of an undescribed species of *Nothria* (family Onuphidae) are present on rhizomes and between blades of *Thalassia*, on pieces of bark (Sts P844 and P1178), and on *Sargassum* (P187) from altogether 8 stations. The tubes are 24–28 mm long, hyaline, and partly covered with tests of pelagic foraminiferans and small mollusc shells (Pl. 1F).

On bark (St. P338) was found a species of Maldanidae in a semitransparent tube, with many very small and a few larger tests of foraminiferans of pelagic origin. Serpulidae were present on a large lump of wood (Pl. 1E), on a *Nothria* tube on bark (Pl. 1F), and on wood (St. P53); they represent two, perhaps three species (K. Fauchald pers. commn).

**Mollusca: Gastropoda: Turridae.** Three empty capsules and one filled with eggs, all on *Thalassia*, belong to two turrid species. A third species (St. P675) is represented by one empty capsule on a leaf (Pl. 2A) and two capsules on bark (one with eggs).

**Bivalvia: Mytilidae.** Many specimens of *Modiolus abyssicola* are attached with their byssus to wood (St. P526). Three other, bathyal species of *Modiolus*, 1.5–4 mm long, are from the Caribbean area (Sts P1435, P1178, P719, and P844) and from St. P53 in the Gulf of Guinea (Pl. 1G). Another four mytilids are from St. P328 in the Caribbean.

**Crustacea: Cirripedia.** In addition to a stalked barnacle of the deep-sea genus

Table 2. Known instances of organisms utilizing plant material in the deep sea (almost exclusively > 1200 m, except for echinoids). Number of localities in brackets. A question mark in front of the name indicates that the reference is somewhat doubtful, a question mark after the name that a deep-sea origin of the organism is not quite certain. References to illustrations on plates in this paper in italics.

Group	Area and No. of localities	Depth (m)	Plant material	Utilizing as	Reference
			Wood Thalassia Others	sub- strate ter food	
Foraminiferida					
1	<i>Cibicides</i> sp. Caribbean (3)	1326-4417	. + .	+ ?+	WOLFF 1979
2	<i>Cyroidina</i> sp. " (1)	2450	+ . .	+ . .	This paper
3	<i>Tiphotrecha</i> sp.? " (5)	1373-2450	+ . .	+ . .	This paper, Pl. 1B
4	Allogromiida Off Georgia (1)	2288	. + .	+ ?+	WOLFF 1979, fig. 1b
5	?Foraminiferida Caribbean (2)	2450,4417	. + .	+ ?+	WOLFF 1979, fig. 1e
Xenophyophoria					
6	<i>Semipsammia fixa</i> Puerto Rico Trench (1)	5890-6000	. + .	+ . .	WOLFF 1976:163, fig. 1B
7	Spongia Off California (1)	2073	+ . .	+ . .	MURAOKA 1966:21, fig. 9
Coelenterata					
8	Hydrozoa " (1)	"	+ . .	+ . .	MURAOKA 1966:21
9	Hydrozoa Caribbean	Deep water	Plant remains	+ . .	SOUTHWARD 1972:763
Octocorallia					
10	?Stolonifera New Britain Trench (1)	8260	+ . .	+ . .	LENCHÉ et al. 1976:276, pl. 8a
Actinaria					
11	?Actiniidae " (1)	"	+ . .	+ . .	LENCHÉ et al. 1976:277
12	<i>Bathyaetylus ?waldiviae</i> Caribbean (3)	4180-6800	. + .	+ . .	WOLFF 1976:163, fig. 1C,E
Turbellaria					
13	? <i>Xenoborgia</i> n.sp. " (1)	3852	. + .	+ . .	WOLFF 1979; Pl. 1C
14	<i>Fecampia</i> sp. " (1)	1760	+ . .	+ . .	This paper, Pl. 1D
15	Acocela? " (1)	4417	. + .	+ ?+	WOLFF 1979
Entoprocta					
16	Loxosomatidae N. Atlantic	1836	+ . .	+ . .	OCKELMANN in Litt.
17	Nematoda Caribbean	Deep water	Plant remains	. ?+	SOUTHWARD 1972:763
18	Polychaeta " "	"	"	. ?+	SOUTHWARD 1972:763
19	Polychaeta Puerto Rico	8000	. . sugar cane	. ?+	GEORGE 1978
20	Polychaeta Celebes Sea	2053	+ . .	. ?+	WEBER 1902:63
21	Polynoidae, Lepidonotinae Iberian Basin (1)	5260	+ . .	. + .	H. THIEL in Litt.
22	<i>Harmothoe ingolfiana</i> N. Atlantic (1)	1836	+ . .	. + .	This paper
23	<i>Palaemonotus</i> sp. Gulf of Guinea (1)	1549	+ . .	. + .	This paper
24	Phyllocoridae, Pareteoninae Iberian Basin (1)	5260	+ . .	. + .	H. THIEL in Litt.
25	Hesionidae, Hesioninae " (1)	"	+ . .	. + .	H. THIEL in Litt.
26	Hesionidae, ? <i>Nereimyra</i> N. Atlantic (1)	1836	+ . .	. + .	This paper
27	<i>Miarophthalmus</i> sp. " (1)	"	+ . .	. + .	This paper
28	<i>Neanthes bioculata</i> Iberian Basin (1)	5260	+ . .	. + .	H. THIEL in Litt.
29	<i>Neanthes sandiegensis</i> Off S. California (1)	728-855	+ . .	. + .	FAUCHALD 1977:158, pl. 1a,b
30	<i>Nereis anoculis</i> " "	1383	+ . .	. + .	FAUCHALD 1977:160, pl. 2
31	<i>Nereis profundii</i> Banda Trench (1)	7250-7290	. . <i>Pandanus</i>	. + .	KIRKEGAARD 1956:68, fig. 4
32	<i>Nereis caymanensis</i> Cayman Trench (2)	5800-6850	. + <i>Spartina</i>	. + .	WOLFF 1976:167, fig. 2F
33	" " Caribbean (1)	4580	. . Coconut	. + .	This paper, Pl. 4N
34	<i>Nereis</i> sp. " (2)	1517, 1760	+ . .	. + ?+	This paper
35	<i>Nereis</i> sp. Gulf of Guinea (1)	1549	+ . .	. + ?+	This paper
36	<i>Glycera tessellata</i> Caribbean (1)	1760	+ . .	. + .	This paper, Pl. 2B
37	<i>Nothria</i> n.sp. " P. Rico Tr. (7)	1656-7471	+ + .	. + .	WOLFF 1979, [fig. 1i-k, 2b,d; Pl. 1F]
38	<i>Ophryotrocha</i> sp. N. Atlantic (1)	1836	+ . .	. + .	This paper
39	<i>Laonice cf. bahusiensis</i> " (1)	"	+ . .	. + .	This paper
40	Cirratulidae sp. A " (1)	"	+ . .	. + .	This paper
41	Cirratulidae sp. B " (1)	"	+ . .	. + .	This paper
42	Cirratulidae sp. C Caribbean (1)	1517	+ . .	. + .	This paper
43	? <i>Cirratulus</i> sp. " off Georgia (2)	1517, 2288	+ + .	. + .	WOLFF 1979, fig. 4b
44	Capitellidae sp. A N. Atlantic (1)	1836	+ . .	. + .	This paper
45	Capitellidae sp. B Caribbean (1)	1517	+ . .	. + .	This paper

Reference 19 should read GEORGE & HIGGINS 1979.

Group	Area and No. of localities	Depth (m)	Plant material			Utilizing as		Reference		
			Wood	Thalassia	Others	sub-shel- strate	ter food			
46	Capitellidae sp. C	Cayman Trench (1)	6800	.	+	.	.	?	This paper	
47	Maldanidae	Caribbean (1)	1827	+	.	.	+	.	This paper	
48	Maldanidae	" G.of Guinea (4)	1517-1650	+	.	.	.	+	This paper	
49	<i>Muggoides striatus</i>	Caribbean (1)	1517	+	.	.	.	+	This paper	
50	<i>Muggoides</i> sp.	Gulf of Guinea (1)	1549	+	.	.	.	+	This paper	
51	<i>Thelepus?</i>	" (1)	"	+	.	.	.	+	This paper	
52	Sabellidae, Fabriciinae	Caribbean (1)	1517	+	.	.	.	+	This paper	
53	Serpulidae sp. A	" Cayman Tr. (2)	1656,6740	+	.	.	+	.	This paper, PL. 1E	
54	Serpulidae sp. B	Gulf of Guinea (1)	1549	+	.	.	+	.	This paper	
Sipuncula										
55	<i>Golfingia schuttel</i>	Caribbean, off Guiana (2)	1517,1253	+	.	.	.	+	This paper, PL. 2F-H	
56	<i>Phascolosoma</i> n.sp.	" (1)	1128-1178	+	.	.	.	.	M. RICE in litt.	
Echiura										
57	<i>Kurchatovus tridentatus</i>	" P.Rico Tr. (3)	4580-6780	+	+	Coconut	.	.	+	WOLFF 1976:167; {PL. 4V,W PL. 5A,B
Mollusca										
58	Polyplocophora	Celebes Sea (1)	2053	+	.	.	.	.	?	WEBER 1902:63
59	<i>Lepidopleurus</i> sp. A	Caribbean (1)	6740-6780	+	.	.	.	.	?	This paper, PL. 5C
60	<i>Lepidopleurus</i> sp. B	" (1)	1650	+	.	.	.	.	?	This paper
61	Gastropoda	" (?)	Deep water			Plant remains	?	?	?	SOUTHWARD 1972:763
62	Acmaeidae	" (1)	4374	+	.	.	.	.	?	This paper
63	<i>Pectinodonta arcuata</i>	" (1)	775	+	.	.	.	.	?	This paper
64	<i>Pectinodonta maxima</i>	Bay of Biscay (1)	4459	+	.	.	.	.	+	This paper
65	Trochidae	Gulf of Panama (1)	3197	+	.	.	.	+	.	This paper
66	Cocculinidae	" (1)	"	+	.	.	.	.	?	This paper
67	Cocculinidae n.gen.	Caribbean (1)	1650	+	.	.	.	.	?	This paper, PL. 5H
68	<i>Caymanabyssia spina</i>	Cayman Trench (2)	6740,6800	+	.	Straw	.	.	?	This paper, PL. 5D
69	<i>Fedikovella caymanensis</i>	" (2)	"	+	.	.	.	.	?	This paper
70	<i>Fedikovella</i> n.sp. 1	" Carib. (2)	2970-5280	.	.	Coconut	.	.	?	This paper
71	<i>Fedikovella</i> n.sp. 2	" (1)	7950-8100	+	.	.	.	.	?	This paper, PL. 5G
72	<i>Pseudococculina</i> n.sp. 1	" Carib. (4)	3700-6780	+	.	Coconut	.	.	?	This paper, PL. 5E,F
73	<i>Pseudococculina</i> n.sp. 2	" (1)	6800	+	.	.	.	.	?	This paper
74	Fam. nov. 1	" P.Rico Tr.(4)	5220-6780	.	+	.	.	.	+	WOLFF 1976:167, fig. 2K
75	Fam. nov. 2	Caribbean (3)	2450-4417	.	+	.	.	.	+	This paper, PL. 5J
76	Turridae	Gulf of Panama (1)	3197	+	.	.	.	+	.	This paper
77	Turridae capsule A	Off Guiana (1)	1253	.	.	?Leaf	+	.	.	This paper, PL. 2A
78	Turridae capsule B	Cayman Trench (1)	6740-6780	.	+	.	+	.	.	WOLFF 1979, fig. 1g
79	Turridae capsule C	Off Georgia (1)	2288	.	+	.	+	.	.	WOLFF 1979, fig. 1h
80	Opisthobranchia	Caribbean (1)	1760	+	.	.	.	+	.	This paper
81	Bivalvia	" (?)	Deep water			Plant remains	?	?	?	SOUTHWARD 1972:763
82	Arcidae	Celebes Sea (1)	2053	+	.	.	+	.	.	WEBER 1902:63
83	<i>Aca* asperula</i>	Mindanao Sea (1)	1500	+	.	.	+	.	.	KNUDSEN 1970:74, fig. 46.
84	Mytilidae	Caribbean (2)	1517-2071	+	.	.	+	.	.	This paper
85	<i>Modiolus abyssicola</i>	Panama Gulf, N.W.Pac. (4)	1750-3670	+	.	.	+	.	.	This paper
86	<i>Modiolus</i> sp. A	Caribbean (1)	1650	+	.	.	+	.	.	This paper
87	<i>Modiolus</i> sp. B	" (1)	1760	+	.	.	+	.	.	This paper
88	<i>Modiolus</i> sp. C	" (2)	1517,1656	+	.	.	+	.	.	This paper
89	<i>Modiolus</i> sp. D	Gulf of Guinea (1)	1549	+	.	.	+	.	.	This paper, PL. 1G
90	<i>Myrina longissima</i>	E.Ind.Ocean, W.Pac. (2)	1143,1500	.	.	Coconut	+	.	.	KNUDSEN 1961:206
91	<i>Myrina coppingeri</i>	S.W.Pacific (1)	2560	.	.	Pl.debris?	?	.	.	KNUDSEN 1961:206
92	<i>Idasola argentea</i>	N.Atlantic (3)	944-1836	+	.	.	+	.	.	JENSEN 1912:56, pl. 3, 3a-e.
Pholadidae										
93-117	<i>Xylophaga</i> (25 deep-sea spp.)	Most seas	ca.200-7290	+	.	Rope	.	.	+	KNUDSEN 1961:203
118	<i>Xylophaga knudseni</i>	S.W. of Japan (1)	3100	+	.	.	.	.	+	OKUTANI 1975:73
119	<i>Xylophaga rhyabtschikovi</i>	Scottia Sea (1)	1660	+	.	.	.	.	+	KUD.-PASTERNAK 1975:180, fig. 1
120	<i>Xylophaga clenchi</i>	Ctr.-N.Atlantic (?)	300-1836	+	.	.	.	.	+	TURNER 1970:66
121	<i>Xylophaga</i> n.sp.	Off New England (1)	1830	+	.	.	.	.	+	TURNER 1973:1377, fig. 2
122	<i>Xylophaga</i> ? species	Caribbean (5)	1373-4180	+	+	.	.	.	.	WOLFF 1979; PL. 5K,L
123	<i>Xylophaga</i> ? species	" G.of Guinea (7)	1253-1760	+	.	Straw	.	.	+	This paper, PL. 5M

Group	Area and No. of localities	Depth (m)	Plant material			Utilizing as		Reference		
			Wood	Thalassia	Others	sub-strate	shel-ter		food	
124	<i>Xylorodo noot</i>	Off Bahama Islands (1)	1737	+	.	.	.	+	TURNER 1972a:5, pls 1,2	
125	<i>Xylorodo naeoli</i>	Off California (1)	2073	+	.	.	.	.	TURNER 1972a:10, pls 5,6	
126	<i>Xylorodo ingolfia</i>	N. & N.W. Atlantic (2)	1830-1836	+	.	.	.	.	TURNER 1973:1377	
127	<i>Xylopholas alternai</i> Teredinidae	Florida, Ctr.W.Afr. (6)	239-72550	+	.	Coconut	.	.	+	TURNER 1972b:104, figs 1-12
128	<i>Baukia carinata</i> <sup>1</sup>	Banda Sea (1)	7250-7290	.	.	<i>Pandanus</i>	.	.	+	TURNER 1966:56
129	<i>Uperotus clavus</i> <sup>1</sup>	" (1)	"	.	.	<i>Pandanus</i>	.	.	+	TURNER 1966:56
130	<i>Teredothyra smithi</i> <sup>1</sup>	Sulu Sea (1)	5050	+	.	.	.	.	+	TURNER 1966:56
131	<i>Lyrodus bipartita</i> <sup>1</sup>	Gulf of Panama (1)	3270-3670	+	.	.	.	.	+	TURNER 1966:56
132	<i>Notoveredo norvegica</i> <sup>1</sup>	Off Scotland (1)	944	+	.	.	.	.	+	TURNER 1966:56
Crustacea										
133	Copepoda, Harpacticoida Cirripedia	Caribbean (1)	1517	+	.	.	.	.	+	This paper
134	<i>Araoscalpellum</i> sp.	" (2)	4417, 4450	+	+	.	+	.	.	WOLFF 1979; PL. 2C
135	? <i>Verruca</i>	Gulf of Panama (1)	915	+	.	.	+	.	.	This paper
136	Tanaidacea	Caribbean (1)	4580	.	+	.	+	.	.	WOLFF 1976:163
137	Isopoda/Amphipoda	Palau, New Britain Tr., Solomon Trench (ca. 10)	7057-8662	+	Seagrass	.	+	.	2+	LEMICHE et al. 1976:283, pls 13-15, 18, 31
138	Isopoda/Amphipoda	Puerto Rico Trench (1)	2068	2+	.	.	+	.	2+	HEEZEN & HOLL. 1971:239, fig. 7.7
139	Isopoda	Celebes Sea (1)	2053	+	.	.	.	+	.	WEBER 1902:63
140	Isopoda	Caribbean (?)	Deep water	Plant remains	.	.	.	2+	.	SOUTHWARD 1972:763
141	Janiridae	" (1)	1517	+	.	.	.	+	.	This paper, PL. 3B
142	Janiridae n.gen.	" (1)	"	+	.	.	.	.	+	This paper
143	<i>Katianira</i> n.sp.	" (1)	4580	+	+	.	.	.	+	This paper, PL. 3D
144	<i>Janira operculata</i>	Gulf of Panama (1)	3270-3670	+	.	.	.	+	.	WOLFF 1962:44, fig. 7
145	<i>Haploniscus</i> n.sp.	Puerto Rico Trench (1)	7430	.	2+	.	.	2+	.	WOLFF 1979
146	<i>Heteromesus</i> n.sp. A	" (2)	7430-8330	.	+	.	.	+	.	WOLFF 1979
147	<i>Heteromesus</i> n.sp. B	" (1)	7938	.	+	.	.	.	+	WOLFF 1979; PL. 3E
148	<i>Heteromesus</i> n.sp. C	Caribbean (1)	4417	.	+	.	.	+	.	WOLFF 1979; PL. 3E
149	<i>Macrostylis</i> n.sp.	Puerto Rico Trench (1)	7965	.	+	.	.	+	.	WOLFF 1979
150	<i>Echinothambema</i> n.sp.	Caribbean (3, 75)	5800-6850	.	+	.	.	+	.	WOLFF 1979, fig. 6a; PL. 3A
151	Nannoniscidae n.gen. A	" (1)	6800	.	+	.	.	+	.	WOLFF 1979; PL. 2J
152	Nannoniscidae n.gen. B	Puerto Rico Trench (1)	8330	.	+	.	.	+	.	WOLFF 1979, fig. 6d
153	? <i>Austroniscus</i> n.sp.	Caribbean (1)	6840-6850	.	+	.	.	+	.	WOLFF 1979; PL. 2K
154	<i>Bathyporus nybelini</i>	Tasman Sea, P.Rico Tr.(2)	4400, 5850	.	.	<i>Sargassum</i>	.	.	+	WOLFF 1962:239, 244, pls 10, 18
155	<i>Paropsurus giganteus</i>	Tasman Sea (1)	4400	.	.	Algae	.	.	+	WOLFF 1962:243, pl. 11
156	Amphipoda	S.Caribbean (?)	Deep water	Plant remains	.	.	.	2+	2+	SOUTHWARD 1972:763
157	? <i>Atylidae</i> , ? <i>Calliopidae</i>	Off California (1)	2073	+	.	.	.	+	2+	MURAKA 1966:21, fig. 15
158	<i>Onesimoides chelatus</i>	Celebes Sea (3)	1264-4970	+	.	? <i>Nipz</i> fruit	.	.	+	BARNARD 1961:44, figs 12, 13
159	<i>Onesimoides</i> n.sp.	Off Georgia (1)	2288	.	+	.	.	.	.	WOLFF 1979; PL. 5N
160	<i>Lysianassidae</i> ?n.gen.	Caribbean (1)	4580	.	.	Mangrove	.	.	+	This paper
161	<i>Paranesimoides lignivorus</i>	Celebes Sea (1)	2053	+	.	.	.	.	2+	PIRLOT 1933:143, fig. 46
162	<i>Parargissa galathea</i>	S.W.Indian Ocean (1)	4360	2+	.	?Algae	.	.	+	BARNARD 1961:56, fig. 24
163	<i>Oradarea shoemakeri</i>	S. of Java (1)	525	2+	.	.	.	.	2+	PIRLOT 1934:201, fig. 83
164	<i>Bathyaeradoacus stephensi</i>	Celebes Sea (1)	1165-1264	2+	.	.	.	.	2+	PIRLOT 1934:229, fig. 97
165	"	Gulf of Panama (1)	3270-3670	+	.	.	.	.	.	BARNARD 1961:109, fig. 76
166	<i>Bathyaeradoacus iberiensis</i>	Iberian Basin (1)	5315	+	.	.	.	.	+	ANDRES 1977:58, fig. 1
167	<i>Melita lignophila</i>	Gulf of Panama (1)	915	+	.	.	.	.	2+	BARNARD 1961:111, fig. 77
Decapoda										
168	<i>Munidopsis vicina</i>	" (1)	3270-3670	+	.	.	.	+	.	This paper
169	<i>Munidopsis hendersoniana</i>	" (1)	915	+	.	.	.	+	.	This paper
170	? <i>Munidopsis</i> sp.	Puerto Rico Trench (1)	3988	+	.	.	.	+	.	HEEZEN & HOLL. 1971:248, fig. 7.17
171	<i>Xylopagurus</i> sp.	Mindanao Sea (1)	1500	+	.	.	.	+	.	This paper
172	Thalassinidea	"	"	+	.	Coconut	.	+	.	This paper
Brachiopoda										
173	? <i>Terebratulidae</i>	N.Solomon Trench (1)	7847-8662	+	.	.	.	+	.	LEMICHE et al. 1976:283, pl. 16a,b
Echinodermata										
Crinoidea										
174	<i>Bathycrinus australis</i> Asteroidae	Palau Trench (1)	8021-8042	.	.	?Seagrass	+	.	.	LEMICHE et al. 1976:284, pl. 31c

Group	Area and No. of localities	Depth (m)	Plant material			Utilizing as sub-shel-ter	Reference			
			Wood	<i>Thalassia</i>	Others					
175	<i>Hyphalaster inermis</i>	S. of India (1)	4040	+	.	.	.	7+	MADSEN 1961:71, pl. 3	
176	<i>Caymanostella spinimarginata</i>	Cayman Trench (1)	6740-6780	+	.	.	+	.	2+	This paper, Pl. 1E,H
177	<i>Caymanostella</i> sp.	E. of New Zealand (1)	1270-1280	+	.	.	.	.	+	This paper
178	<i>Marginaster</i> n.sp.	Caribbean (1)	1650	+	.	.	+	.	2+	This paper, Pl. 2D
179	Ophiuroidea	Celebes Sea (1)	2053	+	.	.	.	2+	2+	WEBER 1902:63
180	<i>Amphioptera bullata</i>	Off New England (24)	3000-5000	.	.	<i>Sargassum</i>	.	.	2+	SCHOENER & ROWE 1970:923
181	<i>Bathypectinura heros</i>	Bahama Islands (1)	2000-3000	.	+	"	.	.	2+	This paper
Echinoidea										
182	<i>Hygrosoma hoplacantha</i>	E. of Japan (1)	1320	.	.	Kelp	.	.	+	OKUTANI 1969:35, pl. 2,2
183	<i>Hygrosoma petersi</i>	Bahama Islands (1)	2000-3000	.	+	<i>Sargassum</i>	.	.	+	This paper
184	<i>Hygrosoma luculentum</i>	Celebes Sea (1)	ca.400	.	.	Land plants	.	.	+	MORTENSEN 1938:226
185	<i>Hapalosoma pellucidum</i>	Banda Sea (1)	?	.	.	"	.	.	+	MORTENSEN 1938:226
186	<i>Araeosoma splendens</i>	" (1)	300	.	.	Algae	.	.	+	MORTENSEN 1938:227
187	<i>Araeosoma tessellatum</i>	Philipp., Banda Sea (6)	268-400	.	.	Leaves	.	.	+	MORTENSEN 1935:249, pls 36-39
188	<i>Araeosoma fenestratum</i>	N. Atlantic (1)	584	.	.	Algae	.	.	+	MORTENSEN 1938:226
189	"	Caribbean (1)	200-290	+	.	Leaves	.	.	+	LEWIS 1963:361
190	<i>Pygmaeosidaris prionigera</i>	Molucca Sea (1)	1960	.	.	Land plants	.	.	+	MORTENSEN 1938:227
191	<i>Micropyga tuberculata</i>	Banda Sea (several)	ca.200-400	.	.	Land plants	Algae	.	+	MORTENSEN 1940:152, pls 4-9
192	<i>Micropyga violacea</i>	Off Philippines (1)	ca.800	.	.	"	.	.	+	MORTENSEN 1940:157, pls 7-9
193	<i>Plesiodiodema indicum</i>	Banda Sea (1)	290	.	.	"	.	.	+	MORTENSEN 1940:39, pl. 1,1-4
Pogonophora										
194	<i>Sclerolimum minor</i>	Caribbean (8)	470-1285	+	.	.	.	.	+	SOUTHWARD 1972:765, figs 12-14
195	<i>Sclerolimum major</i>	" (6)	470-1470	+	.	.	.	.	+	SOUTHWARD 1972:767, figs 14-15
196	<i>Sclerolimum brattstromi</i>	Norwegian fjords (11)	100-870	+	.	Rope, etc.	.	.	+	WEBB 1964:47, figs 1-7
Tunicata										
197	<i>Cnemidocarpa bythia</i>	S. of Kerguelen	4200-4225	+	.	.	.	+	.	This paper, Pl. 2E
Pisces										
198	<i>Coryphaenoides armatus</i>	Off New Jersey (2)	2580-2780	.	.	<i>Sargassum</i>	.	.	2+	HAEDRICH & HENDERSON 1974:742
199	"	Off Oregon	2700-4000	.	.	<i>Zostera</i>	.	.	7+	PEARCY & AMBLER 1974:750
200	<i>Thaumatichthys binghami</i>	Caribbean (1)	1271	.	.	<i>Sargassum</i>	.	.	2+	BERTELSEN 1977:29, pl. 2
Miscellaneous										
201-205	5 unidentified organisms	" (5)	2450-7965	+	.	"	.	+	.	WOLFF 1979, fig. 2e,f

1. Alive when collected. A shallow-water species which apparently is able to survive for some time in the deep sea, but is unable to reproduce there.

*Arcoscalpellum* on a rhizome (Pl. 2C), the base of another specimen of probably the same species is attached to wood (St. P1444). Five barnacles, probably of the genus *Verruca*, are attached to bark (*Galathea* St. 754).

Tanaidacea. A tube with a small paratanaid was found on a *Thalassia* blade; it has since been lost (F.A. Pasternak pers. commn).

Echinoderma: Asteroidea. A 5 mm specimen of *Marginaster* n.sp. (family Poraniidae) was almost hidden in a cavity in wood at St. P1435 (Pl. 2D). The stomach contained tiny shell fragments, probably of *Xylophaga*.

Tunicata: Ascidiacea. A 9 mm wide specimen of the widely distributed species *Cnemidocarpa bythia* (family Styelidae) was found

attached to a root (Pl. 2E) in the South Polar Sea (C. Monniot pers. commn).

Miscellaneous. A few organisms from *Thalassia* are not referable to major taxa; they include, e.g., flattened hyaline structures and a fragmentary organism with a spongelike, gritty texture.

#### *Animals using plant material as shelter*

Annelida: Polychaeta. The most diversified animal group in the plant material studied is the polychaetes, comprising 16 families and at least 29 different species (Table 2); all species from the Caribbean area, except perhaps *Thelepus*, are deep-water forms (K. Fauchald pers. commn).

A *Xylophaga*-bored piece of a pine log, c. 15 × 35 cm, from *Ingolf* St. 67 in the North

Atlantic (1836 m), contained polychaetes which according to the late A. Eliason's preliminary identifications belong to no less than 9 species and 6 families (K.W. Ockelmann pers. commn). There are many *Microphththalmus* sp. (family Hesionidae) and *Ophryotrocha* sp. (family Dorvilleidae) and from 1-7 specimens of the remaining 7 species (Table 2). *Harmothoe ingolfiana* was described by DITLEVSEN (1917) from *Ingolf* St. 67, but its occurrence in the wood was not mentioned.

The Pillsbury material contained almost 20 species which are being studied by K. Fauchald. Wood from St. P719 in the southern Caribbean yielded no less than 8 species.

Two specimens of *Palaenotus* sp. (family Chrysopetalidae) are from cavities in wood at St. P53 in the Gulf of Guinea. A 40 mm long *Glycera tessellata* (family Glyceridae) was found in wood at St. P1178 (Pl. 2B).

Two thick oval Cirratulidae (probably the genus *Cirratulus*) were situated in an old *Xylophaga* burrow in a rhizome at St. P120 (WOLFF 1979, fig. 4b); other specimens of this species were found in wood at St. P719. A different cirratulid species also came from this station.

There are three specimens of Capitellidae and three of Maldanidae from wood at St. P719. Two species of the deep-sea genus *Muggoides* (Ampharetidae) are present in wood: one *M. sinctus* from St. P719 and five *M.* sp. from St. P53. The terebellid *Thelepus* sp. in wood from St. P53 may not be of deep-sea origin. Finally, one fabriciian sabellid was found in wood at St. P719.

**Sipuncula.** Three specimens of the rather widespread deep-sea species *Golfingia* (*Phascoloides*) *schutteii* were found in wood: one in a mud plug in an old *Xylophaga* cavity at St. P675 (Pl. 2F), one in a crevice in wood, and one inside a twig (St. P719). The latter presents a problem. When the bark was removed, the worm was found in a cavity, surrounded by mud (Pl. 2G). It was not noted whether or not there was a small hole in the bark above the cavity. This has obviously been excavated by some animal (Pl. 2H), and so has neighbouring, smaller, partly mud-filled cavities without any occupants (Pl. 2G). It would seem that either the sipunculan entered the cavity which had been gnawed under the bark by another, later vanished animal, filled the cavity with mud and was able to stretch the proboscis out through a possible hole in the bark, or, while growing to

its present size, the worm excavated the cavity itself.

*Golfingia pellucida* and some other sipunculans are able to form burrows in calcareous rock, possibly by a chemical solvent produced by the epidermal glands and by rubbing the substrate with papillae of the trunk and the posterior shield (CUTLER 1973; RICE 1969). An abundant, new *Phascolosoma* which is being described (M.E. Rice pers. commn) is wood-boring but furnished with numerous hooks on the anterior introvert. Although *G. schutteii* has small spines or hooks on the introvert, it is not likely that it is able to bore in wood, unless this is softened by some unknown enzyme (M.E. Rice and E. Cutler pers. commn). Unfortunately, an examination of gut contents cannot be performed, since after identification the sipunculans were lost in the mail.

**Mollusca: Gastropoda.** Inside wood from St. P526 are three small specimens of Trochidae and two of Turridae. A tiny, left-coiled shell from wood (St. P1178) is an opisthobranch. A *Thalassia* rhizome from St. P1168 contained a pelagic young of *Tonna maculosa* which must have reached the bottom with the rhizome (M. Rex pers. commn); it was tentatively identified as 'perhaps a "rissoid" type of gastropod' (WOLFF 1979, fig. 4h).

**Crustacea: Copepoda.** A few harpacticoid copepods were found in *Xylophaga*-bored wood from St. P719.

**Isopoda.** Isopods proved to be the most abundant group of animals inside *Thalassia* rhizomes: in all, 55 specimens belonging to 9 species were found (WOLFF 1975, 1979). From five stations, mainly at hadal depths, were no less than 55 *Echinothambema* n.sp. (Pl. 3A), 45 of which were still inside rhizomes, while at least some of the remaining have certainly been washed out before examination.

The genus *Heteromesus* (family Ischnomesidae) is represented by 5 beautifully preserved specimens of 3 undescribed species occurring exclusively in *Thalassia* rhizomes (Pl. 3E, F). GEORGE (1979) also found *Heteromesus* in plant debris from the Puerto Rico Trench. None of the altogether 34 records of the 12 previously known species of this deep-sea genus have mentioned any relationship with plant material.

One specimen of Macrostylidae (*Macrostylis* n.sp.) and 2 very small specimens of Nannoniscidae (belonging to 2 undescribed genera) were also found inside rhizomes (Pl. 2J). So was



one specimen (Pl. 2K) of altogether 6 representatives of another new species of *Nanoniscidae* (cf. *Austroniscus*) from two stations. Finally, one specimen of *Haploniscus* may or may not have come from a rhizome (WOLFF 1979).

In addition to the wood-feeding janirid isopod (p. 126), a different, 1.2 mm long, janirid isopod was found below the bark of a twig, also at St. P719 (Pl. 3B); the pale, almost transparent gut indicates that it probably does not eat wood.

Two adults (nearly 3 mm long) and one juvenile of *Katianira* n.sp. (family Janiridae), with spines on the flattened legs (Pl. 3D), were found in two old *Xylophaga* burrows in a 13 cm long mangrove radicle from St. AK1272 (Pl. 3C). Judging from the position of the animals they may feed on the wood. A fourth specimen was inside a *Thalassia* rhizome from the same station.

**Decapoda.** At *Galathea* St. 716 in the Pacific were collected 13 small specimens of the squat lobster *Munidopsis vicina*, two of which were found in holes in a tree trunk. A similar habitat was noted for three small specimens of altogether seven *M. hendersoniana* from *Galathea* St. 745 in the same area.

The hermit crab *Xylopagurus* was using a piece of bamboo as shelter at 1500 m in the Mindanao Sea (*Galathea* St. 443) from where also two specimens of burrowing *Thalassinidea* were recorded, one extracted from a coconut husk, the other from a piece of wood.

#### *Animals using plant material as food*

**Gnawing activity.** At almost all stations many *Thalassia* rhizomes and blades show unmistakable signs of having been gnawed or bitten by animals which only in the case of boring bivalves and perhaps fish, echinoids, and amphipods are identifiable to group. The Pillsbury material comprised c. 600 pieces of rhizomes (average length 5 cm) and c. 200 pieces of blades (average length 10 cm) of which 52 and 35 %, respectively, showed traces of recent gnawing activity (WOLFF 1979).

The most common type of rhizome gnawing is carried out more or less deeply from the ends (Pl. 3G, H); sometimes gnawing extends from old *Xylophaga* burrows (3J). More or less superficial gnawing is also common, both on fresh rhizomes and on old ones which are hollow inside (3K-M).

Blades are mainly gnawed or bitten along the margins or at the ends, some traces being scat-

tered, semicircular or more closely set bites (Pl. 4A, B, F), others more resembling those originating from continuous gnawing by smaller animals (4C). Gnawing along the edge may be combined with surface gnawing (4D); the latter may be much decayed or of recent origin (4E) or has been carried out from the edge of a sharply bent blade (4G).

The most important grazers of seagrass beds in the Caribbean area are echinoids, fishes, and, at least locally, amphipods. The former group comprises three species, one *Tripneustes*, one *Diadema*, and one *Lytechinus* (RANDALL 1965). At Jamaica *L. variegatus* consumes about 50 % of the production of *Thalassia* (GREENWAY 1976). About 20 of more than 200 fish species studied had seagrass as a minor part of their diet, and 8 species mainly fed on seagrass (RANDALL 1965, 1967). They include the three surgeonfish species (*Acanthurus*) and some of the abundant parrotfishes (*Scarus* and *Sparisoma*). Seagrass-feeding amphipods at Florida include species of *Cymadusa*, *Gammarus*, *Melita*, and *Grandidierella* (ZIMMERMAN in press).

The scattered, semicircular bites on the blades from the deep sea closely resemble those being made by the parrotfish *Sparisoma radians* (GREENWAY 1976). Other, less uniform and less symmetrical bite marks may originate from echinoids (J.A. Rivera and R.J. Zimmerman pers. comm.). At least part of the continuous edge-gnawing and superficial gnawing of blades, consisting of small bites, is probably due to the shallow-water feeding activity by amphipods, described by ZIMMERMAN (in press). However, as far as rhizomes are concerned, there is no evidence that they form part of the diet of any shallow-water organism. It is therefore likely that the extensive gnawing of rhizomes mentioned above was mainly carried out by deep-sea animals, probably mainly amphipods or gastropods or both.

*Sargassum* was rare in the collection studied; a few leaves were gnawed (Pl. 4H, J). Apart from burrows of boring bivalves, traces of gnawing of woody material were rather scarce (4K).

**Annelida: Polychaeta.** Three specimens of a new species, *Nereis caymanensis* (FAUCHALD 1977) are related to other deep-water species of the genus. They were found in the Yucatan Basin (St. AK1272) in a coconut husk and in the Cayman Trench (Sts AK1243 and AK1259) in a *Spartina* straw and inside a

*Thalassia* rhizome; all specimens had plant material in their gut. Four specimens of (? another) *Nereis* were extracted from wood at bathyal depths (Sts P719 and P1178) and probably a third species came from wood at St. P53 in the Bay of Guinea, but information on the gut contents is not yet available.

A small, unidentifiable specimen of Capitellidae from a rhizome in the Cayman Trench (St. AK1242A) has the gut filled with fragments which closely resemble *Thalassia* tissue.

**Echiura.** Five specimens of a very peculiar new echiurid genus and species, which will be described by DATTA GUPTA (in press), were found in wood in the Puerto Rico Trench (St. AK1187), in wood and in a *Thalassia* rhizome in the Cayman Trench (AK1267), and in a coconut husk in the Yucatan Basin (AK1272). The worms are furnished with two enormous, tridentate hooks (WOLFF 1979, fig. 4d-f), and gut contents clearly indicate that they feed on the plant material in which they live (Pl. 4L). One specimen had excavated most of the wood under the bark of a twig, which in addition to the worm and hooks of two deceased specimens contained a lot of woody debris (Pl. 4M). Burrows were gnawed by the specimens in a piece of wood and a coconut husk (Pl. 5A, B).

**Mollusca: Amphineura: Chitonidae.** On the large lump of wood from the Cayman Trench, 6740 m, were 39 chitons up to about 25 mm long (Pls 1E, 5C), and in a cavity in wood (St. P1435, 1650 m), a 3.5 mm long specimen; they probably represent two new species of *Lepidopleurus* (R.C. Bullock pers. commn).

**Gastropoda: Acmaeidae.** A small specimen was taken from wood at St. P631. In the Bay of Biscay at 4500 m several *Pectinodonta maxima* have been found on pieces of wood; they leave scars on the wood and probably feed on it (P. Bouchet pers. commn). Also some *P. arcuata*, dredged in the South Caribbean at 775 m, are from wood (J.H. McLean pers. commn).

**Cocculinidae** (and related forms). Two new genera, *Caymanabyssia* and *Fedikovella*, have so far been described from the Cayman Trench (MOSKALEV 1976): more than 200 specimens of *C. spina* (Pl. 5D) on the large lump of wood and on twigs and straw at St. AK1267 and 3 specimens from a twig at St. AK1242A; altogether 39 specimens of *F. caymanensis* on wood from the same two stations. The number of specimens of the other 5-6 cocculinid species from wood,

listed in Table 2, are as follows (L. Moskalev pers. commn): No. 66: 11; No. 67: 5 (Pl. 5H); No. 70: 2; No. 71: 11 (Pl. 5G); No. 72: 17 (Pl. 5E-F); No. 73: 1. The 11 specimens of No. 74 were found exclusively in *Thalassia* rhizomes at 4 stations (WOLFF 1976) and belong to a yet undescribed family related to the Cocculinidae. Finally, 14 specimens were also found in rhizomes, at 3 stations; they belong to another new family, of the order Planilabiata (L. Moskalev pers. commn). It was obvious that some of these specimens were feeding on the loose marrow (Pl. 5J; WOLFF 1979, fig. 4b, d), while others were occupying burrows, some of which at least originated from boring bivalves (Pl. 5H; WOLFF 1979, fig. 5c).

Recent investigations in the Puerto Rico Trench (GEORGE & HIGGINS 1979) have revealed many additional cocculinid-like gastropods. They are abundant also at shallower depths; in 1970, the *Oregon II* collected numerous specimens at 8 stations (500-775 m) in the southern Caribbean (E. Southward pers. commn).

**Bivalvia: Pholadidae.** Before I borrowed plant remains from the Pillsbury cruises, much wood with live bivalve borers had been sent to Ruth Turner, M.C.Z., Harvard, for study. Nevertheless live Xylophagainae were found in wood from 7 stations in the present collection (P1435, P1178, P719, P905, P682, P675, and P53), 1253-1760 m. Almost 50 g of straws of a monocotyledonous plant, 5-12 mm wide, were also heavily attacked by *Xylophaga*, almost entirely in the vicinity of the knees (Pl. 5M).

A total of 11 live specimens and many dead shells and empty burrows in *Thalassia* rhizomes from 5 Pillsbury stations, 1373-4180 m (WOLFF 1979, fig. 5g-k), are the first records of Xylophagainae in seagrass. Some rhizomes are so heavily attacked that the burrows are of considerable length (Pl. 5K, L). Two live and 5 dead specimens have brood protection with 1-5 juveniles (Pl. 5K and WOLFF 1979); all known brooding species of *Xylophaga* occur in deep water (TURNER & CULLINEY 1970).

The present Pillsbury material is being studied by Ruth Turner, but unfortunately details on e.g. number of species are not available.

**Crustacea: Isopoda.** A 2.5 mm long isopod, with a feltlike appearance and strong spines on the flattened legs, was situated in a burrow between the bark and the wood of a twig at St. P719. The burrow had obviously

been gnawed by the isopod and was filled with finely masticated wood. The species seems to belong to a new genus of Janiridae.

**A m p h i p o d a .** One *Onesimoides* n.sp. of the family Lysianassidae (J. Just pers. commn) was found at the end of a burrow which extended along the outer surface of a *Thalassia* root and through the base of some scale leaves (Pl. 5N).

The mangrove radicle from St. AK1272 (Pl. 3C) in which three isopods (*Katianira*) were found also contained an unusually small lysianassid amphipod (c. 2 mm long). It was situated in a self-gnawed cavity, filled with tiny wood fragments. It is related to the genera *Onesimoides* and *Paronesimoides*, but may belong to an undescribed genus (J. Just pers. commn).

**E c h i n o d e r m a : A s t e r o i d e a .** On the large lump of wood from the Cayman Trench, 6740 m, were 12 specimens of sea-stars, measuring 9.5 mm in diameter (Pl. 1E, H). They were described as *Caymanostella spinimarginata* of the new family Caymanostellidae within the phanerozoan sea-stars (BELAYEV 1974). However, the species appears rather to be a representative of the family Asterinidae within the Spinulosa (F.J. Madsen and A. Dartwell pers. commn). The edges are furnished with a row of small, close-set spines which may aid in attaching to a hard surface such as wood. A probably different species of *Caymanostella* has just been found on submerged wood off New Zealand at 1270 m; according to A. Dartwell, three of fifteen specimens had wood fragments in the mouth cavity (see Addendum, p. 136).

## DISCUSSION

Transportation of plant material to the deep sea

Particularly large amounts of plant remains have been reported from Indonesian waters, the Gulf of Bengal, and the Gulf of Panama (WEBER 1902; BRUNN 1959). Most records are from basins in the vicinity of land and often off the mouths of large rivers. However, on the *Galathea* we came across floating roots or logs far from land on at least three occasions, and the log recovered by the *Ingolf* (p. 117) must also have travelled a long distance before sinking. On board the *Akademik Kurchatov*, on one occasion I observed large quantities of floating fragments of twigs, bark, and straw (up to 2-3 pieces per m<sup>2</sup>).

Blades of *Thalassia* and other seagrasses in the Caribbean area are detached by feeding of fish and echinoids (RANDALL 1965; GREENWAY 1976) and by wave action. Storms, particularly hurricanes, uproot whole plants which may be washed ashore in enormous quantities (THOMAS & al. 1961; MOORE 1963). Perhaps equally large quantities are washed out to sea. Observations of rafts of drifting turtle grass (up to 50 m in diameter) were made after a hurricane (MENZIES & al. 1967). Larger amounts were photographed on the bottom just after the hurricane season than six months later and had been transported 550 to 1100 km before being deposited (MENZIES & ROWE 1969). Rafting or current-carried transport and subsequent sinking were also believed to be the reasons for the broad distribution of turtle grass in the Virgin Island Basin (ROPER & BRUNDAGE 1972).

The occurrence of green grasses wrapped around telegraph cables (ERICSON & al. 1952) and of buried debris (*Halimeda*, leaves, and wood) in cores from various basins and trenches (HEEZEN 1955; HEEZEN & al. 1955; ANIKOUCHINE & LING 1967) show that turbidity currents are important in bringing shallow-water sediments and vegetal matter to the great depths. A down-slope movement may also be responsible for the high concentration of turtle grass recorded at the base of the continental slope off North Carolina by MENZIES & ROWE (1969).

## Abundance

Based on data supplied by MENZIES & ROWE (1969) on the distribution of *Thalassia* blades, an estimation of average numbers of blades per photo (covering 6.35 m<sup>2</sup> bottom) was attempted (WOLFF 1979). About 50 blades per photo were recorded on the Blake Plateau (MENZIES & al. 1967), and more than 10 blades per photo were observed in hundreds of the 5300 photographs examined by ROPER & BRUNDAGE (1972); however, in neither case were the areas covered per photo stated.

A much higher concentration prevails in the Tongue of the Ocean, a 2000-3000 m deep 'fjord' in the shallow Great Bahama Bank. Photographs analyzed by P. Polloni and N. Staresinic showed that 1.2 % of the total area surveyed (900 m<sup>2</sup>) was covered with a layer of detrital *Thalassia* (WOLFF 1979, fig. 6i).

R.L. Haedrich, Woods Hole, has kindly sup-

plied me with details of plant material trawled (with a 40' GMT, 1 hour tow) in connection with studies of the fish fauna off New England. Of a total of 36 collections (1871–4986 m), at least 26 contained *Sargassum* and/or eelgrass (*Zostera*) and small amounts of beach grasses. Wood was present in 19 collections. The plant matter was weighed at most stations. The average wet weight of *Sargassum* and *Zostera* amounted to 500 g per station, the maximum value being 6200 g (at 4099 m). The average wet weight of wood was almost 200 g, two collections (at 3300 and 4621 m) amounting to 1500 and 1250 g, respectively.

The quantities dredged by the *Akademik Kurchatov* and the *Pillsbury* are recorded in Table 1. The gear used by the former was a 3 m sledge trawl, and the estimated time on the bottom was about one hour. The *Pillsbury* used a 41 foot otter trawl, usually working for 2 hours on the bottom at depths down to about 4500 m and for 4 hours at greater depths (G.L. Voss pers. commn).

The samples of wood, etc., were not measured on the *Kurchatov* and those from the *Pillsbury* are minimum values (p. 118).

By far the largest samples of *Thalassia* occur in the trough-shaped Puerto Rico and Cayman Trenches (Table 1) and in the Yucatan Basin (St. AK1272), which is close to extensive turtlegrass beds along the adjacent Mexican coast. This abundance obviously reflects transportation by slumping or turbidity flows or both rather than by the rafting method mentioned above. This assumption is supported by observations during recent investigations in the Puerto Rico Trench (GEORGE & HIGGINS 1979). They revealed particularly large amounts of plant debris in the Gilliss Deep, which apparently serves as a trap for material brought down with turbidity flows.

#### Utilisation of plant material as a substrate

Hard substrates are generally scarce in the deep sea. Rock outcrops and manganese nodules, as well as pumice, cinders, waterlogged wood, and other foreign objects, have previously been known to serve as convenient substrates for epifaunal animals. Seagrass blades and rhizomes are apparently also significant in this respect, 16 different organisms having above been shown to utilize these substrates. A similar number of

species used woody material. Adding the scattered and not easily detectable records in the literature (Table 2), a total of about 50, mainly sessile, deep-sea organisms have been found to make use of plant material as a substrate.

Most common are the byssus-producing bivalves of the family Mytilidae (Table 2). JENSEN (1912) counted about 260 specimens of *Idasola argentea* in crevices and cavities of a piece of pine wood from 1836 m depth in the North Atlantic; this species was also present in great numbers on and in panels of wood submerged for 3½ months off New England at 1830 m (TURNER 1973). The 4 known records of the East Pacific *Modiolus abyssicola* are all from wood (KNUDSEN 1970; OKUTANI 1975; above p. 119).

#### Utilization of plant material as shelter

HARTMANN-SCHRÖDER (1975) recorded a number of polychaetes from the Iberian Basin without mentioning the substrate. Four species (Table 2, Nos 21, 24, 25, and 28) were from wood (H. Thiel pers. commn); the three first were too fragmentary to allow identification to genus.

Polychaeta is the dominating group seeking shelter in wood. Four polychaete species have already been shown to eat wood (p. 125), and a detailed study may show that some of the more than 25 additional species (Table 2) are also herbivorous.

Three of the 5 known species of *Sclerolinum*, a bathyal genus of Pogonophora, have exclusively been recorded from organic material. Two were found abundantly in more or less soft rotten wood and mats of roots (SOUTHWARD 1972) and the third in all sorts of wood, in rope or on pieces of cardboard and leather (WEBB 1964).

The fact that *Thalassia* rhizomes were the preferred habitat for almost all the 55 specimens of the isopod *Echinothambema* found at 5 stations might suggest that the species is herbivorous, but this was not supported by gut examinations (WOLFF 1979). The scarcity of specimens of the remaining 9 or 10 species of isopods found mainly in *Thalassia* did not allow a study of the gut contents.

Including the few previous records, about 43 deep-sea species have been shown to utilize plant remains primarily as shelter. In addition, the majority of the herbivores mentioned below live inside the plant material on which they feed.

## Utilization of plant material as food

*The trophic role of organic material in shallow water Seagrasses.* It is generally agreed that detritus, mainly derived from the benthic macrovegetation, is of major importance as a link between primary and secondary production in shallow-water areas. Seagrass beds are one of the most productive biological systems known; they are widely distributed both in boreal and tropical soft-bottom regions and typically produce between 500 and 1000 g C/m<sup>2</sup>-yr, but only a few consumer species are known to utilize seagrass directly (FENCHEL 1973). Microorganisms have been shown to constitute the real food source of detritus consumers, rather than the nutritional-poor residues of vascular plants. Such consumers are the polychaete *Cirriformia tentaculata*, the molluscs *Hydrobia ulvae*, *H. ventrosa*, and *Macoma balthica*, the amphipods *Parhyalella whelpleyi*, *Corophium volutator*, and *Gammarus oceanicus*, and the mullet *Mugil cephalus*, which utilize almost exclusively the microflora associated with the detritus, while the detrital particles themselves pass nearly unchanged through the intestine (GEORGE 1964; NEWELL 1965; FENCHEL 1970, 1972; HARGRAVE 1970, HARRISON 1977; ODUM 1970). Similarly, zooflagellates, amoebae and ciliates, associated with detritus, feed exclusively on bacteria or on other protista (FENCHEL 1968, 1970), as do groups of micrometazoans such as turbellarians and rotifers (STRAARUP 1970; THANE-FENCHEL 1968). Various fungi constitute the food of the nematode *Aphelenchoides* (MEYERS & al. 1963), while the nematode *Metoncholaimus* accumulates abundantly and reproduces in substrates covered by fungal hyphae (MEYERS & HOPPER 1966).

Thus, the only primary decomposers of macrophyte tissue are bacteria and fungi. They synthesize all cellular materials including proteins, lipid, carbohydrates, ectocrine compounds, etc., which make up the bulk material of detritus, and concentrate and assimilate dissolved inorganic nitrogen and phosphorus from the sea water. While the biomass of fungi on detritus is not known, FENCHEL (1970, 1973) found between 10<sup>9</sup> and 10<sup>10</sup> bacteria per gram dry weight detritus of 4 × 10<sup>-3</sup> g. This biomass is typically of the same order of magnitude as that of zooflagellates and ciliates, the two major groups of protozoans feeding on bacteria (FENCHEL & HARRISON 1976). Enrichments with

inorganic nutrients increased both the density of bacteria and bacterivorous protozoans and the rate of decomposition, while protozoan grazing reduced the density of bacteria with about 50 % but had a decidedly stimulating effect on the rate of decomposition (FENCHEL & HARRISON 1976, HARRISON & MANN 1975). Similarly, the amphipod *Parhyalella*, feeding on *Thalassia* detritus and its own fecal pellets, increased the microbial oxygen uptake by nearly 100 % in 92 hours (FENCHEL 1970), and two *Gammarus oceanicus* increased the rate of decomposition of *Zostera* leaf particles by 35 % in 24 days (HARRISON 1977). The amphipods stir the particles and markedly reduce their average size, thereby increasing the total surface area and subsequent microbial activity.

**Wood.** Biodeterioration of wood is mainly performed by bacteria and fungi which produce extracellular enzymes destroying the material and by molluscs and crustaceans which bore into the material which they ingest and may subsequently utilize.

Bacterial attack on submerged wood was reported on by IRVINE & al. (1972). KADOTA (1956) isolated and identified bacteria from sea water; thirty species were able to degrade pure cellulose under laboratory conditions. Bacteria also seem to be responsible for the breakdown of cellulose in the stomach of the shipworm *Teredo navalis* (ROSENBERG & CUTTER 1973 and previous papers). Because of the unbalanced C:N ratio of cellular nitrogen in shipworms, nitrogen fixation by bacteria in the gut also takes place (CARPENTER & CULLINEY 1975).

The cellulolytic activity of marine fungi was described by MEYERS (1968), JONES (1971), and EATON & JONES (1971). Wood-boring isopods (*Limnoria*) produce cellulase in the intestine (RAY & JULIAN 1952), but for complete development and propagation *L. tripunctata* depends on additional nutrients, probably mainly proteins and vitamins, provided by lignicolous marine fungi (KOHLMAYER & al. 1959). RAY & STUNTZ (1959) were unable to find fungi in wood attacked by *Limnoria*; this is probably due to the difficulty in recognizing the presence of soft-rot fungi, which cause tunnels inside the cell walls (J. Kohlmeyer pers. commn). Preliminary experiments have shown that the amphipod *Gammarus mucronatus* reproduced and lived for months exclusively on a diet of various fungi (R.V. Gessner pers. commn).

The most important wood-boring animals are

molluscs and crustaceans. The former comprise about 22 species of shallow-water Pholadidae and nearly 70 species of Teredinidae. Among the crustaceans, chelurid amphipods (3 species) and limnoriid isopods (about 20 species) are true wood-borers, while sphaeromatid isopods bore into wood for shelter rather than for food.

Checklists of marine, potentially lignicolous fungi, cellulytic bacteria, and wood-boring molluscs and crustaceans are provided by JONES & al. (1976).

#### *Decomposition of organic material in the deep sea*

**Fungi.** At least four and possibly six species of Ascomycetes and Deuteromycetes of deep-sea origin (at depths between 1600 and 5315 m) are known at present (MURAOKA 1966; KOHLMAYER 1968, 1969, 1977). All species cause 'soft rot', a destruction similar to that caused by higher fungi in terrestrial, freshwater, and shallow marine habitats.

All the numerous deep-sea wood samples studied by KOHLMAYER contained fungal mycelia, but the majority had no reproductive structures. The same applies to wood panels submerged for less than two years off California. This seems to indicate a very slow development of fructifications.

**Bacteria.** MURAOKA (1966, 1971) and KOHLMAYER (1969) found that cellulytic bacteria were present in all wood specimens examined (panels submerged at 720–2075 m and driftwood at 3270–3670 m). Decay starts in the tertiary cells, and finally all wall layers are transformed into an amorphous mass of wood remnants. Cotton and manila ropes, submerged for 6.3 months at 1800 m, lost nearly 50 % of their original strength due to bacterial activity (MURAOKA 1971).

A much lower microbial degradation was demonstrated in *in situ* experiments at depths between 1830 and 5300 m off New England, following the observation of a strikingly well-preserved state of waterlogged food materials recovered with the sunken research submersible *Alvin* (JANNASCH & al. 1971; JANNASCH & WIRSEN 1973, 1977; WIRSEN & JANNASCH 1976). Solid organic materials, including algae, tree leaves, wood, bread, fish meat, etc., decomposed 10–100 times more slowly in the deep-sea environment than the refrigerated controls, and deep-water populations converted the substrates 17–125 times faster when incubated in the

laboratory at 3° C than *in situ* at 1830 m in closed containers. SEKI & al. (1974), on the other hand, found that in an enriched deep-sea sample incubated *in situ* at 5200 m, the organotrophic activity of rod-shaped bacteria was nearly the same as that exhibited in shallow water.

The rate of degradation depends on the site of incubation and the kind of material, but particularly on whether the substrates are encased or exposed to attack by the macrofauna (amphipods, boring bivalves), causing disruption of tissue and increase of particle surface area (SIEBURTH & DIETZ 1974; WIRSEN & JANNASCH 1976).

#### *Plant material as a source of food for the deep-sea macrofauna*

Several authors (particularly MURRAY 1895; MORTENSEN 1938; HEEZEN & al. 1955; BRUUN 1959; KNUDSEN 1961; WOLFF 1962; MENZIES & al. 1967; ROPER & BRUNDAGE 1972) have noted organic remains as a probable source of energy in the deep sea. ROWE & MENZIES (1969) suggested a correlation between the occurrence of suspended *Thalassia* detritus and three suspension feeders, and an indication of holothurians being more abundant where *Thalassia* is plentiful was noted by ROPER & BRUNDAGE (1972) and N. STARESINIC (G.T. Rowe pers. commn).

The present investigation has demonstrated an abundance of apparently fresh traces of gnawing activity both on rhizomes and blades of seagrass. Gastropods are presumably responsible for most traces on the rhizomes.

The most frequent feeders on *Thalassia* are the boring bivalves: *Xylophaga* or closely related genera. In addition to the eleven live specimens and the large number of dead shells recovered from burrows, a great many empty burrows in rhizomes bore witness to heavy attacks.

It is noteworthy that no *Xylophaga* have been found in the large number of rhizomes from great depths in the Puerto Rico and Cayman Trenches (Table 2). This agrees with the fact that KNUDSEN (1961) found only two species in wood from the hadal zone.

A remarkable species diversity within wood-boring *Xylophaga* has been demonstrated by KNUDSEN (1961), and panels placed in the deep sea become heavily infested within a few months (MURAOKA 1966; KOHLMAYER 1969; TURNER 1972a, 1972b, 1973).

The geographical distribution of Xylophagainae is dependent on the presence of suitable plant material and the dispersal ability of the free-swimming larvae. These may be able to delay metamorphosis, and either be produced in great numbers and carried by bottom currents, or, more likely, be able to detect wood or seagrass and actively swim towards it. The high reproductive rate of the Xylophagainae, their high population density, rapid growth, early maturity, and utilization of a transient habitat classify them as opportunistic species, the first recorded from the deep sea (TURNER 1973).

The diversity and abundance of cocculinid gastropods demonstrated above (p. 126) are also significant: In the Caribbean and the Puerto Rico Trench at depths exceeding 2500 m, 25 specimens (2 species) were found in *Thalassia* rhizomes at 7 stations, and about 300 specimens (at least 7 species) occurred in and on wood and coconuts at 11 stations. Although actual evidence of feeding on the substrates is available only in a few cases (p. 126), there can hardly be any doubt that all cocculinids occurring on organic remains utilize them as food. The abundance of cocculinids may justify regarding them as another example of opportunistic species in the deep sea.

The acmaeid limpets and chitons recorded from wood may also be herbivores like most of their shallow-water relatives. It is quite likely that both the cocculinid and acmaeid gastropods and the chitons utilize a cover of microbial organisms (see below) rather than the substrate; deep-sea chitons possibly feed on organic material removed from the surface of manganese nodules (PAUL 1976).

The numerous species of echinoids feeding on land plants and algae, which were mentioned by MORTENSEN (see Table 2, Nos 184-188 and 190-193), have since been the classical example of deep-sea herbivores. However, apart from a few species, herbivorous echinoids are all from the upper part of the bathyal zone.

The concentration of the sea-star *Caymanostella spinimarginata* and *C. sp.* on wood (p. 127) and fragments of wood inside the latter strongly suggest that they feed on this substrate or on a cover of microorganisms or both. MADSEN (1961) found a 23 mm long twig in the stomach of a porcellanasterid, *Hyphalaster inermis*. Two, apparently feeding, sea-stars (Goniasteridae) were photographed on a ?carcass and seagrass blades (LEMICHE & al. 1976).

The same applies to brittle-stars. SCHOENER & ROWE (1970) found *Sargassum* bladders in 1 % of many *Amphiophiura bullata*, but believed that the epifaunal ectoprocts were the major source of nutriment rather than the plant. A dense and diversified echinoderm fauna has been observed at 2000-3000 m in the Tongue of the Ocean, Bahamas, in an area with large quantities of *Thalassia* (D.L. Pawson pers. commn); preliminary examination of gut contents has revealed *Thalassia* and *Sargassum* in a few brittle-stars (*Bathypsectinura heros*) and in the echinoid *Hygrosoma petersi*. WEBER (1902) and H. Thiel (pers. commn) noted ophiuroids as one of the animal groups associated with plant remains in the Indonesian and Iberian deep sea, respectively. There are no convincing examples of shallow-water ophiuroids selectively feeding on plants (FELL 1966).

Six species of deep-sea amphipods are definitely herbivorous: *Onesimoides* n.sp. uses *Thalassia* (p. 127), *O. chelatus* was extracted from a piece of wood (PIRLOT 1933) and later found abundantly feeding on fruit meat of a *Nipa* palm (BARNARD 1961), an *Onesimoides*-like lysianassid eats mangrove (p. 127), 25 specimens of *Bathyceradocus stephensi* and two of *B. iberiensis* were found in wood and had wood fragments in the gut, and *Paragissa galathea* had wood or algae in the gut (BARNARD 1961; WOLFF 1962; ANDRES 1977). Another five species were extracted from wood (Table 2, Nos 156, 157, 161, 163, 167); they probably also use this substrate as a source of food.

It is interesting that both known species of *Bathyceradocus* and two of the four known species of the deep-sea genus *Onesimoides* are recorded as herbivores. However, these two and the four other genera referred to in Table 2 belong to five different families.

There are three certain instances of herbivorous deep-sea isopods: specimens of *Bathyporus nybelini* and *Paropsurus giganteus* (the largest known asellote isopods) had their guts entirely or partly filled with masticated *Sargassum* and (less frequently) fucalean algae (WOLFF 1962), and a janirid species is a wood-borer (p. 126). It is possible that the three other species of Janiridae from wood and some of the nine or ten species of isopods from *Thalassia* (Table 2) are also herbivores, but this could not be verified (pp. 124-125).

The feeding habits of the sipunculan *Golfingia schuttei* are likewise uncertain. An abundant

wood-boring sipunculan has recently been found in the Caribbean deep sea (M.E. Rice pers. commn). Equally unexpected is the present discovery of the wood-boring echiuran *Kurchatovus* (p. 126), encountered both in wood, a coconut husk, and *Thalassia*.

So far there are five certain instances of herbivorous polychaetes: an undeterminable capitellid with woody fragments in the (transparent) gut; three *Nereis caymanensis* whose guts contained the substrate in which the specimens were found (coconut husk, *Spartina* straw, and *Thalassia* rhizome); several *N. profundus* which were extracted from a *Pandanus* fruit from the Banda Trench (KIRKEGAARD 1956) and which have later been found to have the guts filled with plant debris; *N. anoculis* and *Neanthes sandiegensis* from logs and also with plant remnants in their guts (FAUGHALD 1977). A closer examination of the other specimens of *Nereis* from wood (p. 126) and of the many other polychaete species now under study may show that at least some of them are also herbivorous.

Finally, the fragments of *Sargassum* and *Zostera* recorded from stomachs of a macrourid and a ceratioid fish species (Table 2) have probably been ingested accidentally; fragments of seagrass are also occasionally found in stomachs of predaceous fish in shallow water (RANDALL 1965).

The availability of wood, seagrass, etc., for the specialized deep-sea herbivores mentioned above is probably rather constant in deep-sea areas within a reasonable distance from river mouths and extensive shallow-water growths of seagrass. No doubt a mass occurrence, particularly of seagrasses, is furthered by hurricanes (p. 127), but it is likely that once on the bottom, blades and rhizomes are available for the herbivores for a considerable time, since on the whole degradation seems to be slow (JANNASCH & al. 1971; JANNASCH & WIRSEN 1973, 1977; KOHLMAYER 1969).

Only a few data on the potential energy of organic material in deep water are available. Carbon contents in clumps of *Thalassia* at about 2300 m depth at the Bahama Islands were found to be more than twenty times higher, and nitrogen contents ten times higher than in sediments not associated with *Thalassia* (G.T. Rowe pers. commn; WOLFF 1979). Caloric values for *Thalassia* rhizomes and blades from the Caribbean deep sea are about 10 % lower than for

fresh rhizomes and probably also blades (WOLFF 1979); the values for the fresh rhizomes are slightly lower than the average value recorded for leaves of terrestrial plants and for *Zostera* blades, but considerably higher than the values for *Zostera* rhizomes in shallow water.

Similar to the case in shallow-water species, it is unlikely that most deep-sea herbivores are able to directly utilize the nutrients in organic material. Some may, however, be able to produce cellulase, as e.g. *Limnoria* in shallow water.

The presence of symbiotic, cellulolytic bacteria is common in shallow-water herbivores. In deep-sea amphipods, SCHWARZ & al. (1976) and SCHWARZ & COLWELL (1976) have demonstrated the occurrence of an intestinal microflora whose metabolism is not markedly inhibited by *in situ* temperature and pressure.

Fungi and heterotrophic bacteria are the primary decomposers of detrital matter and wood in shallow water and serve as the first link in the food chain of the micro- and macrofaunal consumers of detritus (p. 129). This is certainly also the case in the deep sea, but the importance of the microflora as a source of food is difficult to evaluate.

The deep-sea fungi probably develop fruiting bodies very slowly, but hyphae form rapidly on submerged panels and are always present in wood trawled in the deep sea (MURAOKA 1966; KOHLMAYER 1969, 1977).

The data provided by JANNASCH & WIRSEN (p. 130) indicate an extremely low activity of deep-sea bacteria. The discrepancy of these data and those of MURAOKA, KOHLMAYER, SEKI, and SIEBURTH & DIETZ (p. 130) are probably attributable to various reasons. Firstly, the availability of energy at the sample site is important. In water and sediment samples with low contents of organic matter bacterial activity will be low, while the opposite may be the case where the microorganisms are associated with an energy source. Thus, MORITA (1979) found a good rate of activity in various bacteria causing necrotic lesions in the Tanner crab (*Chionoecetes tanneri*) at depths down to 5000 m. Plant remains represent another available source of energy, but do not represent a balanced diet necessary for all metabolic functions of organisms.

Secondly, in shallow water the rate of degradation is stimulated by macrofaunal consumers which increase the substrate area and the subsequent microbial activity (p. 129). A similar



macrofaunal effect has been demonstrated in the deep sea (SIEBURTH & DIETZ 1974; WIRSEN & JANNASCH 1976); it seems likely that the reason for this effect is also an increased microbial activity in the deep-sea environment.

Finally the apparent age or residence time of deep water masses should be taken into account. Because of the time factor, even low rates of metabolism will permit the bacteria to perform their functions (MORITA 1979). Slow rates of microbial activity reflect the adaptation of microbes to the available energy supply in the environment which also takes into consideration the time factor.

When settling, the larvae of the shallow-water borers *Lyrodus pedicellatus* and *Teredo navalis* distinctly favour wood surfaces which have been softened by the action of cellulytic fungi or bacteria (KAMPF & al. 1959; LANE 1961). If this is also the case in the deep sea the extremely rapid settlement of *Xylophaga* larvae on submerged wood panels (MURAOKA 1966; TURNER 1973) indicates an even faster surface deterioration rate by fungi or bacteria or both.

As in shallow water (p. 129), it is highly probable that fungal mycelia are a direct source of food for some of the herbivores, e.g. isopods and amphipods.

Grazers of bacteria are known to occur in shallow water (p. 129), but very little is known about their presence in the deep sea. UHLIG (1970, 1971) discovered ciliates, turbellarians, gastrotrichs, and archiannelids at depths down to 2000 m and single specimens of the two former groups were isolated from even greater depths and photographed. Large numbers of sarcodines (more than 20 distinct morphological types) and of sporozoan trophozoites were present in sediments at 1130–1200 m off California (BURNETT 1973), and ciliates and other naked protozoans (flagellates and amoebae) were part of the microbiota of a sediment sample from 5500 m in the North Pacific (BURNETT 1977), with an estimated number of 16 500–26 900/cm<sup>2</sup>. A higher link in the food chain is represented by galatheid lobsters which have been observed hunting for smaller crustaceans on submerged panels and which have a remarkable growth rate of from 10 to 35 mm length in 10 months (R. Turner pers. commn).

Available data indicate that decomposition of organic material in the deep sea is performed in the same way and by the same kinds of decomposers as in shallow water, although generally

at a reduced rate. The final link in the decomposition food chain is provided by the macrofaunal herbivores; these not only produce fecal pellets which can be utilized by deposit-feeders but also are available as prey for predators and as dead remains for scavengers.

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PLATES 1-5

#### PLATE 1.

A. Fragments of mainly *Thalassia* rhizomes and blades, some *Cymodocea*, *Sargassum*, bark, and wood, Puerto Rico Trench, 8330 m. — B. Probably live foraminiferans (*Tiphrotrocha* sp.) on wood, north of Cuba, 1650 m. — C-D. Neorhabdocoele turbellarians; *Kronborgia* n.sp. on *Thalassia* root, Caribbean Sea, 3852 m (C) and *Fecampia* n.sp. on a piece of bark, Caribbean Sea, 1760 m (D). — E. Large lump of wood (about 60 × 12 cm) with 10 serpulid polychaetes, 39 chitons (*Lepidopleurus* sp. A), 206 cocculinid gastropods (*Caymanabyssia spina* Moskalev), and 12 sea-stars (*Caymanostella spinimarginata* Belyaev), Cayman Trench, 6740 m. — F. Polychaete, *Nothria* n.sp., in tube attached to bark, off Trinidad, 1656 m. — G. *Modiolus* sp. attached in old *Xylophaga* cavity in wood, Gulf of Guinea, 1549 m. — H. *Caymanostella spinimarginata* Belyaev from wood, Cayman Trench, 6740 m.

#### PLATE 2.

A. Empty gastropod capsule (Turridae) on ?leaf, off Guiana, 1253 m. — B. *Glycera tessellata*, *in situ* in an old *Xylophaga* cavity in wood, Caribbean Sea, 1760 m. — C. Stalked barnacle, *Arcoscappelum* sp. on rhizome, north of Cuba, 2450 m. — D. *Marginaster* n.sp., *in situ* in cavity in wood, north of Cuba, 1650 m. — E. Ascidian, *Cnemidocarpa bythia*, attached to root, South Polar Sea, 4200 m. (Courtesy of C. Monniot, Paris.) — F-H. Sipunculan, *Golfingia schutteii*; with mud ball from old *Xylophaga* cavity in wood, off Guiana, 1253 m (F); in mudfilled cavity under the bark of a twig together with a polychaete, Caribbean Sea, 1517 m (G); same sipunculan, still *in situ* after removal of the mud (H). — J. Nannoniscid isopod *in situ* in rhizome, Cayman Trench, 6800 m. — K. Isopod (cf. *Austroniscus* n.sp.) *in situ* in rhizome, Cayman Trench, 6840 m.

#### PLATE 3.

A. Isopod, *Echinothambema* n.sp., from *Thalassia* rhizome, Cayman Trench, 6800 m. — B. Janirid isopod *in situ* under bark of twig, southern Caribbean, 1517 m. The whitish spots are small lumps of mud. — C-D. Mangrove radicle (C) containing 3 *Katianira* n.sp. (D) and one lysianassid amphipod. — E-F. *Heteromesus* n.spp. C and B *in situ* in hollow rhizomes, northern Caribbean, 4417 m, and Puerto Rico

Trench, 7938 m. — G-H. *Thalassia* rhizomes gnawed at the end only (G, top and H) and right through (G, middle), Sts P1444 and P1401. — J. Gnawing extending from an old *Xylophaga* burrow, St. P120. — K-M. More or less superficial gnawing on fresh rhizomes and on an old, hollow rhizome, Sts AK1181, AK1272, and AK1183.

#### PLATE 4.

A-B, F. Scattered, semicircular fish bites (A-B) and closely set bites in *Thalassia* blades (F), Sts AK1272, AK1267, and P1238. — C. Fresh and old gnawing of blade, St. AK1258. — D. Surface and edge gnawing of blade, St. P905. — E. Much decayed and fresh surface gnawing of blade, St. AK1272. — G. Surface gnawing on the upper and lower surface of a blade which was sharply bent (the edge indicated by arrows), St. P1238. — H-J. Surface and edge gnawing of *Sargassum*, Sts AK1183 and AK1272. — K. Surface gnawing of fruit, St. P1259. — L-M. Echiuran, *Kurchatovus tridentatus*, with wood in the (damaged) gut, hooks of a dead specimen, and the twig (bark partly removed) inside which the worm and the hooks were found, Puerto Rico Trench, 5890-6000 m. — N. *Nereis caymanensis* with coconut husk material in the gut, Yucatan Basin, 4580 m.

#### PLATE 5.

A-B. Burrows made by *Kurchatovus tridentatus* in wood and a coconut husk. — C-D. One of 39 chitons, *Lepidopleurus* sp. A, and one of more than 200 cocculinid gastropods, *Caymanabyssia spina*, from a large lump of wood, Cayman Trench, 6740 m. — E-F. *Pseudococculina* n.sp., *in situ* on a piece of coconut husk, north of Cuba, 4550 m (E) and on a twig, Cayman Trench, 6740 m. (Courtesy of L. Moskalev, Moscow.) — G. *Fedikovella* n.sp., *in situ* on a twig, Puerto Rico Trench, 7950-8100 m. (Courtesy of L. Moskalev, Moscow.) — H. Cocculinidae n.gen. in old *Xylophaga* burrow in wood, north of Cuba, 1650 m. — J. Cap-shaped gastropod of an undescribed family of Planilabiata *in situ* in a cavity gnawed inside a *Thalassia* rhizome, north of Cuba, 2450 m. — K-L. Mature *Xylophaga* with one juvenile and dead shells *in situ* (K) and rhizome with entrance holes to burrows (L), off Georgia, 2288 m. — M. Boring bivalves, *Xylophaginae*, infesting knees of straw, off Guiana, 1737 m. — N. Amphipod, *Onesimoides* n.sp., *in situ* in gnawed burrow in *Thalassia* root.









